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Volume XII
1936

BALTIMORE
THE JOHNS HOPKINS PRESS
1936

Composed and Printed at the
WAVERLY PRESS, Inc.
for
THE JOHNS HOPKINS PRESS
Baltimore, Maryland, U. S. A.

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Vol. 12 No. 1 DECEMBER, 1935 Serial No. 56

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THE EFFECTS OF CEREBELLAR LESIONS UPON THE HABITUATION OF POST-ROTATIONAL NYSTAGMUS

BY
WARD HALSTEAD
Northwestern University

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THE JOHNS HOPKINS PRESS
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THE EFFECTS OF CEREBELLAR LESIONS UPON THE HABITUATION OF POST-ROTATIONAL NYSTAGMUS[1]

WARD HALSTEAD

Northwestern University

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[1] Ph.D. dissertation, Northwestern University, June, 1935. The investigation was conducted in the laboratory of and under the supervision of Prof. Franklin Fearing; major expenses were defrayed from funds granted to him by The National Research Council and by Northwestern University.

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CHAPTER I

The term "extinction phenomena" is a generic term and is commonly applied to behavioral patterns which under appropriate conditions are in process of disappearing from the repertoire of responses of a given organism. Interest in these phenomena has derived chiefly from two schools of thought. One of these has found in "extinction phenomena" support *par excellence* for the point of view which insists that the most stable behavior patterns known, viz. "reflexes," are in actuality both remarkably variable in character and notably susceptible to functional modification (cf. Fearing, 25). The other school, whose proponents are chiefly "reflexologists," has itself discovered that its own favored unit, the "conditioned reflex," may be extinguished in two ways: either by idleness (40) or by over exercise (repeated elicitation, 39).

That a function may be lost through disuse has long been recognized as an important characteristic of the behavior of organisms. However, in the past two decades it has been repeatedly demonstrated that under appropriate conditions a response of an intact organism may be caused to disappear by successive acts of causing it to appear. Needless to say, the emergence of this unfamiliar phase of the problem of organic modifiability has required drastic revision of psychological theory. The result in some instances has been a re-orientation in which "extinction phenomena," such as impairment by repetition, become the most fundamental aspect of behavior modifiability. An example of this newer emphasis may be noted in the following quotation from Razran, 1930 (68):

> The impairment and final disappearance of a pattern upon repetition is then taken as the most general fundamental phenomenon of behavior modifiability, in spite of the large amount of contrary evidence from maze running, poem reciting, problem solving, and the like, for the mere reason that impairment by repetition has been observed in simple reaction-patterns, both native and acquired (salivary, patellar, flexion, lid, postural, vestibular, and psychogalvanic reactions as well as the so-called tropisms of lower animals) and under well controlled conditions, while improvement by repetition has manifested itself in much more complex acts, in which both the activation of more than one pattern and the entrance of more factors than simple repetition are highly probable.

The considerable body of data already available concerning "extinction phenomena" indicates that between the limits of zero frequency (idleness) and the frequency sufficient to extinguish a given response (over exercise) there exists a range of frequencies for elicitation which is optimal for the survival of that response. This fact has considerable significance both for the psychologist and for the physiologist. It dismisses abruptly those "theorists" who postulate in some form a "channeling" or "grooving" process going on in the central nervous system associated with processes usually termed *learning*.

Among the more conspicuous examples of "reflexes" known to be susceptible to marked impairment by repeated elicitation is that generally known as vestibular nystagmus. In man and other mammals vestibular nystagmus is a response to stimulation characterized primarily by a saccadic oscillation of the eyes usually in one plane. In birds, although an ocular deviation may be noted, vestibular nystagmus is primarily a saccadic oscillation of the head through a given plane. In general, nystagmus may be elicited in four different ways: (1) by direct assault upon the non-acoustic labyrinth, (2) by caloric irrigation of the ear, (3) by galvanic stimulation of the middle ear region, and (4) by accelerating or decelerating an organism during angular translation through space. The situation in which the conditions of (4) are most readily satisfied is one involving rotation of an organism about a central axis. Thus the terms "rotational nystagmus" and "post-rotational nystagmus" are commonly employed to designate the response to acceleration and deceleration respectively. It must be kept in mind that the adjectives "rotational" and "post-rotational" when used with nystagmus characterize the incidental rather than the essential conditions related to this response. Equivalent terms sometimes used for these adjectives are the terms nystagmus (acceleration) and after-nystagmus (deceleration).

HEAD NYSTAGMUS IN THE BIRD

The present investigation deals with post-rotational (head) nystagmus in birds, the phenomena of which are described briefly as follows:

At the onset of acceleration there is a drift (lag) of the head in the direction opposite to that of rotation followed by a rapid sweep of the head in the direction of rotation. This is the slow and quick component respectively of rotational (acceleration) nystagmus. Where rotation is prolonged these two components alternate in succession for a period of from five to ten seconds, then disappear. The present investigation has not been concerned with these phenomena.

At the onset of deceleration there is usually an appreciable latent period during which there is no response. This is followed by a drift of the head in the direction of rotation which is terminated by a rapid sweep of the head in the opposite direction. This is the slow and rapid component respectively of post-rotational (deceleration) nystagmus. Under conditions where the animal is deprived of vision these components usually alternate in succession for a period of from eight to thirty seconds before they disappear. Observation of these phenomena has formed the subject of the present investigation.

INVERSE NYSTAGMUS

Under certain conditions (for example, those of the present study) a further phenomenon appears as a part of the after-effect of deceleration, namely *inverse nystagmus.* In approximately 80 per cent of the birds observed during the course of the present study, the phenomena described above as post-rotational nystagmus terminated at some time in a reversal of the directions of the respective components towards those characteristic of rotational nystagmus. In such instances the appearance of *inverse nystagmus* was regarded as the end-point for post-rotational nystagmus. The inclusion here of a reference to this interesting phenomenon is in the interest of completeness of description of nystagmus as it appears in the bird.

THE PHENOMENA OF HABITUATION

The term habituation is used herein to imply the process whereby post-rotational nystagmus is modified in the direction of extinction by repeated elicitations. Experiments which are reviewed below indicate that this modification involves reduction in the number, duration, and amplitude of the nystagmic movements. Of these various factors only changes in the duration of nystagmic movements have been considered in the present investigation. It has been shown that the number of movements is directly proportional to the duration of such movements (Fearing, 1926, 20) but the relationship of each of these to amplitude of movement is unknown.

It is well established that subjecting a group of birds (such as pigeons) to a program of ten or more periods of rotation, with an interpolated rest period of from one-half to two minutes, on successive days for ten to twenty days, will result in a reduction in the duration of after-nystagmus of from 50 to 60 per cent. It is not uncommon to observe half of this amount of reduction appearing at the end of the first day of rotation. Only part of the reduction obtained on a given day carries over and summates with that obtained on successive days. Thus habituation curves usually take the form of a positively decelerated slope for the effects of the first few days of practice, merging into a curve with negative deceleration indicative of diminishing increments of effect associated with further rotational periods. It is this type of curve which is most frequently reported for studies involving "associational learning."

STATEMENT OF THE PROBLEM OF THE PRESENT INVESTIGATION

Although habituation of vestibular nystagmus has been experimentally investigated in various laboratories during the past twenty years, the combined findings do little more than establish beyond question the validity of the phenomena. Comparatively little concerning the nature of the habituation process has been revealed. Most investigators agree that the phenomena are probably "central" in character, but definitive evidence of this fact has not been forthcoming. Decerebrate birds have been found to habituate equally well as birds otherwise deprived of vision. On the other hand, birds rotated while anaesthetized fail to become habituated. This latter finding, published in 1934, offers presumptive evidence that habituation involves a functional modification within the central nervous system; the fact that decerebrate birds become habituated indicates that the process takes place elsewhere than in the cerebral hemispheres.

On the basis of the close phylogenetic and morphological relationships between the non-acoustic labyrinth and the cerebellum the latter structure was regarded as one likely to be directly involved in the habituation process. It was recognized, however, that other attempts to assign particular functions to the cerebellum had uniformly resulted in failure. Thus Magnus concluded in his Croonian Lecture, 1925 (58):

> Unfortunately we know not a single function or reflex positively connected with the cerebellum in such way that it is absent after cerebellar extirpation, and present after ablation of other parts of the brain, as long as the cerebellum remains uninjured.

In relationship with the above facts, the purpose of the present investigation was threefold:

I. It was desired to determine whether the phenomena commonly designated as habituation, which result from repeated elicitation of post-rotational nystagmus, is a process involving modification within the central nervous system.

II. It was desired to determine the effects of cerebellar lesions upon the habituation of post-rotational nystagmus.

III. It was desired to adduce evidence concerning the nature of cerebellar functions.

Following a review of the literature concerning the habituation of vestibular nystagmus and a summary of behavior changes which accompany cerebellar lesions in the bird, evidence is presented in the present report which indicates (1) that habituation is a "central" phenomenon, (2) that the cerebellum is directly involved in the habituation of post-rotational nystagmus by means of repeated elicitation, and (3) that under appropriate conditions the cerebellum may function directly in a process which simulates a "learning" situation.

CHAPTER II

SUMMARY OF THE LITERATURE

Although there is reason to believe that Breuer, 1875 (8) had noted the reduction (or habituation) effect of repeated elicitation of post-rotational nystagmus, there was little attempt to describe this phenomenon prior to Abels, 1906 (1). The use of the Bárány rotational tests for the selection of aviators during the World War (a procedure now known to have been wholly ineffective) precipitated bitter controversies which persisted after the cessation of active combat. These controversies led to the initiation of many experimental investigations of the phenomena of habituation. These latter in turn constitute the immediate background of the present investigation.

An interesting review of the wartime controversy between Army otologists and psychologists over the validity of the phenomenon of habituation has recently been presented by Mowrer, 1934 (62). He has also covered the early history of experimentation in this field, particularly that of the Bárány school (3). Concerning the *post bellum* experiments stimulated by the pointed criticisms of the celebrated Bárány tests made by the above mentioned psychologists, Mowrer's treatment is sometimes lacking in the detail necessary for our purposes. Accordingly we present below a résumé of the major studies since 1920 which have been concerned with the habituation of nystagmus along with additional studies bearing on various aspects of the present general investigation.

THE PHENOMENA OF HABITUATION

Some factors which may influence this process

Griffith, 1920 (33) subjected a group of white rats to continued rotation on successive days over a period of several weeks. For this purpose he used small, circular, individual cages rotating either at 60 or at 90 r.p.m., some in the clockwise and some in the counter-clockwise direction. Duration of nystagmus was found to have shifted from an average of 5.5 seconds after the first rotation to zero after 12 to 18 rotations. Marked equilibratory disturbances were observed in most of his rotated animals. Careful examination revealed that the disturbances were to be attributed to a middle ear disease which had invaded the colony, rather than to any structural modification in the labyrinth associated with continued turning (see Gould).

Griffith also in 1920 (34) reported the results of a similar study made with 16 college students. Each was subjected to a program of repeated daily rotation (physical characteristics unknown), at the end of which average duration of nystagmus had been reduced 79 per cent. His conclusions from this study are quoted below:

> We have discovered then the following facts about the organic effects of rotation, especially about the local effects called nystagmus. We have found that, as turning is repeated from day to day, the duration of the after-nystagmus, the number of ocular movements made, and the duration of the apparent movement rapidly decrease. The major part of this decrease occurs within the first few days. The decrease takes place not only from day to day but also within a period of ten trials, on any single day. The amplitude of the ocular movements and the number of movements made per second also decrease as repetitions increase. Furthermore, certain other organic effects, especially those known as past-pointing, decrease in the same manner. We have also found that the time of nystagmus changes with the speed of rotation and with the number of revolutions and that it is increased when the chair is abruptly halted. As to other conditions under which nystagmus varies in degree and amount, we have found that we must consider: (*a*) the time of day during which rotation is carried on; (*b*) the amount and number of rest-intervals between turnings and between series; and (*c*) the general organic state of the subject. Finally nystagmus may be modified indirectly by "transfer." In general, we have found the organic effects of rotation to be highly variable in their appearance and, moreover, so amenable to practice that they may entirely disappear within a relatively short time, provided rotation is repeated from day to day.

Maxwell, Burke, and Reston, 1922 (59) observed the effect of repeated rotation on the duration of after-nystagmus in the rabbit. These investigators used a specially devised hand-driven rotator rigged with an automatic friction brake, but like many others failed to indicate the stimulus intensity (i.e., rate of angular deceleration) which they employed. Ten rabbits, five rotated with head free and five rotated with head fixed, were given "ten sets of ten turns to the right and ten turns to the left," at the rate of one turn in two seconds over a period of "several" days. Definite habituation was noted in each case and was particularly marked in the animals rotated with the head free. Following habituation these latter were given the caloric test for nystagmus and in each case gave a "perfectly normal response." Maxwell concluded:

> We believe the results warrant the assumption that no injury has been done but that through habituation the organism has been rendered less responsive.

This paper contains a noteworthy observation concerning the specificity of the stimulus pattern:

> It should be mentioned that when the after-nystagmus following rotation at the rate used in these experiments had wholely ceased to appear, a vigorous after-nystagmus could be obtained by using a more rapid rate, say 10 turns in 10 seconds.

Holsopple, 1923 (41) reported some effects of duration and direction of rotation upon habituation. Using groups of male undergraduates he subjected various of them to successive periods of the following rotations: (1) a 25 turn series, (2) a 15 turn series, and (3) a 10 turn series. His data indicated that degree of habituation was directly related to the length of the particular series of turns, being greatest for (1), next greatest for (2), and least for (3). His explanation of this interesting finding was that the "disturbance produced by the acceleration stimulus" had less completely disappeared in the series with fewer turns and thus served to "interfere with the retardation stimulus." This interpretation is supported by the phenomenon of *inverse* nystagmus frequently observed by this writer, further reference to which is made elsewhere. Holsopple found one subject which showed little or no habituation after several days of successive rotations and concluded that the "characteristic drop" is not always present. He also noted that little "recovery" could be detected in two habituated subjects after one month without practice. After a seven months interim, however, one subject showed complete "recovery." Habituation by rotation in one direction was found to have "little effect on the post-rotation nystagmus for the other direction." In a theoretical paper published the same year, 1923 (42) he concluded:

> Rotation in one direction may cause slight reduction in the post-rotation nystagmus of the opposite direction. (This reaction should and probably can be explained in clearer terms than "transfer of training.")

Detlefsen, 1923 (14) modified Griffith's experiment with rats somewhat, using "continuous intermittent" rotation at the rate of 90 r.p.m. for one minute followed by a rest period of one minute. As Griffith had found, his animals showed a marked degree of habituation. Some instances of equilibratory disturbances were encountered but these were later traced to middle ear disease (see Gould, 32). Detlefsen pointed out the significance of labyrinthine infection and noted also a correlation of –.38 (P.E. .014) between the age of his rats and their original readings for post-rotational nystagmus.

Dodge, 1923 (16) devised an ingenious method for photographing eye movements in response to rotation. His results based largely upon himself as subject are in line with those of other observers. Technical difficulties prevented extensive study of the habituation process. He found that oscillation in the direction of rotation did not prevent the appearance of a marked degree of habituation. He also noted that about half the training in one direction had "transferred" to the other direction. Dodge's contribution to the understanding of the problem of habituation has been largely theoretical. Further reference is made to his work in connection with theories of habituation.

Griffith, 1924 (35) tested himself for nystagmus four and one-half years after being habituated to rotation. Griffith was not careful to note the stimulus intensities in any of his experiments, hence his findings are difficult to interpret. His conclusion is as follows:

> The "practice effect" persists for fairly long periods of time. Although the effect may not be apparent in a single turning after a long interval, nevertheless, the time taken to reduce post-rotation nystagmus in a second series is notably shorter than the time taken in the original practice series.

Holsopple, 1924 (43) in a theoretical paper which we mention only briefly at this point concluded:

> With every prolonged rotation, either clockwise or counter-clockwise, both types of nystagmus normally appear. A given type of nystagmus will begin with an acceleration and will stop either because it has run its normal course or because it is interrupted by the stimulus of the opposite type. If a given type of nystagmus is interrupted by the opposite type it counteracts the interrupting nystagmus. Whether one type or the other is decreased by a practice series of rotations in one direction only does not depend on the direction of the practice series but upon the time during which each type of nystagmus occurs.

Dunlap, 1925 (18) modified the procedure used by Maxwell, Burke, and Reston (59) and first studied the habituation to caloric stimulation in two rabbits. Water "within one degree of the temperature of melting ice" was employed for irrigation and was applied through glass tips against the tympanic membrane with a constant force afforded by 70 inches of fall. Each rabbit was given three irrigations on alternate days with a five minute rest period between the second and third irrigations. No nystagmus was produced in one rabbit after the eighth day; in the other none was produced after the eleventh day. When tested for rotatory nystagmus these animals gave responses somewhat shorter than those for normal animals. Dunlap concluded that "the caloric stimulation had produced a certain adaptation to rotatory stimulation also." The effects of the successive irrigations were differentially retained, however. Whereas "no great change in the adaptation against irrigation had occurred during the rest period of six months," little or no retention of rotatory habituation was in evidence at the end of the rest period.

One year later Dunlap and Dorcus, 1926 (19) reported some observations on the effect of rate of retardation on after-nystagmus. Thirty-three male undergraduates were given six rotation periods a day at the same hour of the day and same day of the week for three successive weeks. Three rates of deceleration were used with two observations made for each rate on each test day. For the various rates the rotation chair was brought to a stop in five, seven, and twelve seconds respectively. These investigators concluded:

> To obtain maximum effect upon post-rotation nystagmus: (1) retardation must be made gradual, (2) acceleration should be rapid.

This paper is significant as one of the "early" attempts to demonstrate a relationship between the duration of after-nystagmus and the rate of angular deceleration. Failure to hold this factor constant has resulted in much confusion in the literature.

Fearing, 1926 (20) studied post-rotational head nystagmus in adult pigeons. The rotator consisted of a Maxwell table (59) modified by Fearing and Weymouth (23), the acceleration-retardation characteristics of which were "constant and wholly free from any personal equation of the operator..... The table was so timed that exactly ten turns were made in twenty seconds —a rate which was used throughout the present experiment." After the setting of the automatic friction brake the time required for deceleration was approximately .74 second. Each bird was given ten rotations (ten turns of the table) alternated successively so as to give five clockwise and five counter-clockwise rotations. Vision was excluded by means of a chamois skin hood. Successive rotations followed a rest interval of one and one-half minutes. One hundred and one adult birds ranging in age from two months to two years were used. A correlation of −.20 (P.E. .09) between age and duration of after-nystagmus was obtained for one group of 52 birds. This group of birds differed experimentally from a second group of 49 birds only in the fact that their rotations were begun in the clockwise direction. Yet "striking and consistent differences" were found between the two groups, the "clockwise" group showing greater number of head movements and longer times than the other group. Concerning habituation, Fearing concluded:

> . . . . a consistent reduction of both the number of head movements comprising the post-rotational nystagmus and the duration of the nystagmus is clearly marked. This reduction is made especially striking when it is remembered that it takes place within a single experimental session, usually within a period of less than twenty-five minutes. The reduction is about 30 per cent in the case of head movements, and about 25 per cent in the case of time.

He had previously noted a correlation of .82 (P.E. .02) between number of nystagmic movements and total nystagmus time.

Stoltenberg and Fearing, 1929 (80) reported their observations on the development of after-nystagmus in squabs. These were never published and the data has only recently been summarized by Stone (81). A more detailed reference is made to this work elsewhere in this summary. It is sufficient to note at this point that up to about one month of age there was an age increase in number of nystagmic movements and in nystagmus time in response to rotatory stimulation. After the tenth day of age little change in the susceptibility to habituation was noted.

Huddleston, 1930 (47) recorded the responses to rotation under various conditions of vision for young and for adult pigeons. He used a modified Maxwell table (59) and King's bird holder (51). Rotation was at the rate of one revolution in two seconds, with time for acceleration and for retardation each equal to that for one and one-half turns. His recorded nystagmic patterns showed frequent distortion which he interpreted as due to voluntary head movements. These movements interfered with the duration of after-nystagmus proper. (See also Holsopple, 42.) Huddleston's paper presented no data but the writer reported that adult pigeons were less susceptible to habituation to repeated rotation than were squabs and that the average amount of after nystagmus was considerably greater for adult birds than for squabs. Since the squabs habituated more (and probably faster) than the adults, the number of readings upon which the comparisons were based becomes extremely important. Unfortunately this information was not given.

Ross, Fish, and Axel, 1931 (74) noted the effects of various drugs upon after-nystagmus in dogs. No attempt was made to control deceleration intensity. Nine dogs in all were used, various of which were given "moderate" doses of pilo carpine, nicotine, morphine, and camphor. No change in after-nystagmus was observed after administration of the drugs. Spinal anaesthesia including the body below the neck was found to increase markedly the duration of post-rotational nystagmus, however. Severing the tracts of Goll and Burdock on one side likewise gave an increase in nystagmus. The writers concluded that the spinal cord (chiefly the columns of Goll and Burdock) exerted an inhibitory influence upon vestibular reactions. The results of this study were "loosely" controlled hence must be interpreted with caution.

Mowrer and Casey, 1932 (61) published a note on the relationship between thyroid condition and duration of nystagmus in pigeons. They described the experiment as follows:

> Fourteen healthy adult homer pigeons were carefully tested on three successive days for nystagmus time, weight, and pulse rate. These birds were then equally divided into two groups in such a way that the average value for each of the three items just mentioned was closely comparable for both groups. Beginning on the evening of the third day, one group was force-fed 1/20 gr. of desiccated thyroid every morning and evening for two weeks . . . . The nystagmus time, weight, and pulse rate of each of the fourteen birds were tested every other day during the period of medication. . . .

Body weight remained unchanged (average 14.5 ounces) during the two-week period. By the third day of medication, pulse rate for the experimental group had jumped to 186 beats per minute compared with the control group which averaged 160 beats per minute. No difference in duration of nystagmus nor in degree of the habituation incidentally induced was noted between the groups.

Dorcus, 1933 (17) repeated the experiment performed previously by Griffith (33) and Detlefsen (14), modifying their procedures somewhat.

> A litter of 8 animals (rats) born in a revolving cage were rotated intermittently for 102 days at the rate of one turn a second. The rotation periods were one-half hour in length and the rest periods one and one-half hours.

Little evidence of habituation to rotation could be detected. Dorcus concluded:

> We are of the opinion that marked reduction does not occur in animals unless they are kept in a more or less fixed bodily position. This is certainly true of animals born and reared under the conditions outlined.

It is of interest to note that none of the disturbances of equilibration reported earlier by Griffith and Detlefsen was observed by Dorcus.

Mowrer, 1934 (63) noted incidentally a possible relationship between the treatment given the experimental animals (pigeons) such as hooding, immobilizing by wrapping, etc. immediately preceding the test for nystagmus and the subsequent duration of the after-nystagmus. To test the possibility that animals caught and tested immediately might show longer nystagmus times than birds immobilized and hooded for some time before testing, he alternated these procedures on successive days for ten days with two groups of ten pigeons each. One group had previously been habituated; the other had no previous rotational experience. For both groups the average duration for days on which the birds were immobilized and hooded before testing was found to be significantly shorter. He interpreted the diminished nystagmus of the less "excited" group as being related to "a lowered rate of living" which is reflected by the sensitivity of the non-acoustic labyrinth. (See in this connection paper by Ross and Fearing, 75.)

Mowrer, 1934 (62) in the monograph referred to at the beginning of this summary reported some habituation experiments which he had performed with pigeons. The rotator used was motor driven and starting and stopping were accomplished by the action of electro-magnetic clutches, the time required occupying "about 0.5 second for both directions of rotation." The apparatus was unique in that it was constructed to accommodate six pigeons at once. Repeated rotations under various conditions were given to different groups of "adult pigeons." The conditions included (*a*) rotation of body only with vision excluded; (*b*) rotation of body only with vision permitted; (*c*) rotation of body and environment; (*d*) rotation of environment only; (*e*) rotation with head fixed and vision excluded; (*f*) head fixed and vision permitted; (*g*) six seconds of rotation and fifty-four seconds of rest, and (*h*) fifty-four seconds of rotation and six seconds of rest. The following passage is taken from the summary.

> 1. With the subject's vision excluded and the successive rotation and rest intervals of equal and fairly long duration, repeated bodily rotation in either the clockwise or counter-clockwise direction or alternately in both directions may be relied upon to produce a substantial and equal diminution in both the rotational (acceleration) and post-rotational (retardation) vestibular nystagmus for both directions of turning.
>
> 2. If the conditions described in 1 are varied so as to make the rest (retardation-to-acceleration) interval longer than the rotation (acceleration-to-retardation) interval, repeated bodily rotation in a given direction tends to produce a *greater* reduction in the post-rotational nystagmus for the direction of practice (and in the rotational nystagmus for the unpracticed direction) than in the post-rotational nystagmus for the unpracticed direction (and in the rotational nystagmus for the practiced direction). (This statement is probably true only within limits: thus, if the duration of the successive periods of rotation equals or exceeds the duration of the rotational nystagmus, the differential effect just described cannot be expected to occur.)
>
> 3. If, on the other hand, the conditions described in 1 are varied so as to make the rotation interval longer than the rest interval, repeated bodily rotation in a given direction tends to produce a *smaller* reduction in the post-rotational nystagmus for the direction of practice (and in the rotational nystagmus for the unpracticed direction) than in the post-rotational nystagmus for the unpracticed direction (and in the rotational nystagmus for the direction of practice), although the unavoidable occurrence of an indefinitely long rest period at the end of

each session of repeated rotation tends to make the difference in the reduction of the two types of nystagmus less conspicuous than the difference usually obtained under the conditions described in 2. (This statement, like 2, is probably true only within limits: thus, if the duration of the rest intervals interpolated between the successive rotation intervals equals or exceeds the duration of the post-rotational nystagmus, the differential effect just described cannot be expected to occur.)

4. The particular propositions posited in 1, 2, and 3 may be stated generally, as follows: The longer a given type of vestibular nystagmus is allowed to persist, uninterrupted by an opposing vestibular stimulus, the greater the likelihood that repeated elicitation will reduce the duration and magnitude of this response. (This proposition, previously stated in somewhat different terms by Holsopple (38), should, however, be regarded merely as a descriptive, not as an explanatory concept.)

5. Although vestibular nystagmus may be substantially reduced (about 60 per cent on the average) by means of repeated elicitation with vision excluded, this response cannot, however, be abolished (except, perhaps, at intensities of stimulation considerably weaker or stronger than employed in the present investigation).

6. When the type of subject used in this investigation is rotated with vision permitted, there is a vigorous nystagmus during the entire rotation period but little or no post-rotational nystagmus; repeated bodily rotation either in the clockwise or in the counter-clockwise direction or alternately in both directions does not perceptibly modify this pattern of response.

7. Repeated bodily rotation under the conditions described in 6 likewise does not affect either the rotational or post-rotational vestibular nystagmus produced by bodily rotation in either direction with vision excluded.

8. When bodily rotation is accompanied by concurrent rotation of the visual environment, there is a slight (acceleration) nystagmus at the onset of rotation and a slight (retardation) nystagmus at the end of rotation, both of which responses gradually disappear with repeated elicitation.

9. Repeated bodily rotation under the conditions described in 8, either in the clockwise or in the counter-clockwise direction or alternately in both directions, produces a slight (about 20 per cent on the average) and equal reduction in the vestibular nystagmus elicited during and after rotation in either direction with vision excluded.

10. Rotation of a visual environment around a stationary subject

produces a vigorous nystagmus which lasts as long as the rotation of the environment is continued (or until the subject is fatigued) and which tends to persist for a brief time after the environment has been brought to rest; this persistence of the visually elicited nystagmus after the environment has been stopped gradually disappears with repetition.

11. Repeated elicitation of visual nystagmus under the conditions described in 10, with the successive rotation and rest intervals of equal duration, produces a decided reduction (about 50 per cent on the average) in the post-rotational vestibular nystagmus elicitated by bodily rotation in the same direction as the repeated rotation of the environment, but does not perceptibly modify the post-rotational vestibular nystagmus elicited by bodily rotation in the opposite direction.

12. Repeated bodily rotation in a given direction with vision permitted and head held in a fixed position with reference to the body produces a significant reduction (about 45 per cent on the average) in the post-rotational vestibular nystagmus elicited by bodily rotation in the practiced direction but does not modify the post-rotational vestibular nystagmus elicited by rotation in the opposite direction.

13. Repeated bodily rotation in a given direction, with vision excluded and head held in a fixed position with reference to the body produces a significant (about 35 per cent on the average) and equal reduction in both the clockwise and counter-clockwise post-rotational vestibular nystagmus.

14. Repeated bodily rotation under the conditions described in 13 thus produces less reduction in both types of post-rotational vestibular nystagmus than does similar rotation with the head free.

Fearing and Mowrer, 1934 (26) investigated the effect of general anaesthesia upon the habituation of after-nystagmus. "A standardized test for post-rotational nystagmus" was used for testing and practicing 40 adult common pigeons divided into four groups of 10 birds each. Group I was tested but neither practiced nor anaesthetized; Group II was tested and afterwards anaesthetized on "practice" days but was not practiced; Group III was tested and practiced but not anaesthetized; Group IV (the experimental group) was tested and practiced, but practice was always associated with general anaesthesia induced by appropriate injections of nembutal. Whereas birds in Group III showed marked habituation effects at the end of the 16 day period, no habituation occurred in birds of Group IV. Further reference to this paper is made below.

EVIDENCE WHICH TENDS TO ESTABLISH THE FACT THAT THE MODIFICATION REPRESENTED BY HABITUATION-TO-ROTATION IS "CENTRAL" IN CHARACTER

Abels, 1906 (1) criticized Breuer's interpretation of a structural modification in the labyrinth, pointing out that habituation occurs in a very brief time (hours or days) and that such changes involving little time are usually thought to occur only within the central nervous system.

Maxwell, Burke, and Reston, 1922 (59), reviewed above, found that rabbits habituated to rotation at a certain rate gave a normal nystagmic response to subsequent aural irrigation and to a "faster rate of turning." These investigators concluded that no injury had been done to the end-organ "but that through habituation the organism has been rendered less responsive."

Dunlap, 1925 (18) found that rabbits habituated to caloric stimulation exhibited some evidence of habituation to rotary stimulation as well but observed that these effects were differentially retained. He has also noted that habituation induced by daily irrigations of the left ear had transferred to the response elicited by caloric stimulation of the right ear which had not been previously irrigated. He interpreted this as follows:

> From the marked effect on the right ear nystagmus by left ear irrigation, it is fairly obvious that the adaptation produced by the irrigation was not entirely "peripheral"; that is, it was not an effect on the receptors or other mechanisms within the semicircular canals or vestibules of the ear on the side irrigated; but was in part "central," that is, it was an effect on the nervous mechanism connected with both ears.

Gould, 1926 (32) made a detailed histological analysis of the labyrinths of some of the rats habituated by Griffith (33) and by Detlefsen (14). Gould stated:

> . . . . it early became apparent that a possible structural basis for the abnormal reactions reported must be sought elsewhere than in injury to or abnormal development of the parts of the vestibular ear,

> induced by rotation . . . . the orderly processes of development of the internal ear are shown to be unaffected by the conditions of Griffith's and Detlefsen's experiments.

Gould's analysis included the vestibular ganglia where again no evidence of modification could be noted.

Fearing and Mowrer, 1934 (26) from their experiment in which birds anaesthetized before being practiced failed to become habituated, concluded that:

> In the light of the results of the present investigation and of certain earlier studies cited above, it is evident that the reduction of post-rotational nystagmus, which occurs with repeated elicitation under suitable circumstances, is dependent upon some sort of purely "functional" change in the central nervous system and is in no way due to injury to or structural dearrangement of the vestibular receptors.

While this experiment affords strong presumptive evidence for a central locus of the habituation process it does not preclude the possibility that habituation is associated with "functional overloading" of the receptor, an effect which was probably absent in the anaesthetized birds since the sensory epithelium would likely be affected by the anaesthetic.

EVIDENCE WHICH INDICATES THAT HABITUATION BY REPEATED ELICITATION IS RELATED TO A PERIPHERAL MODIFICATION

There is little direct evidence bearing on this side of the central vs. peripheral controversy.

Breuer, 1875 (6) ventured the suggestion that repeated impact of the endolymph against the hair cells of the epithelium resulted in an increase in elasticity of these cells with progressively less time required for them to return to their normal position.

Steinhausen, 1932 (79) reported that he was able to observe directly movements made by the cupula in response to rotational agitation of the endolymph. "Several" seconds were required for it to resume its normal position. This observation is quite contrary to that of Schmaltz, 1931 (78) who found that the physical processes of the labyrinth lasted only a small part of a second. It should be noted that the existence of the cupula in other than fixed material has been the subject of wide controversy. Even those who affirm its presence in fresh preparations point out the difficulties in observing it directly "because its refractive index differs too little from that of endolymph" (cf. Camis, 9, p. 27).

Huizinga, 1932 (48) observed the gradual disappearance of nystagmic response to galvanic stimulation of the ear in pigeons deprived of their labyrinths but attributed it to the progressive degeneration of the vestibular branch of the VIII nerve precipitated by the operation. In birds in which the labyrinths were rendered functionless by draining off the endolymph no degeneration occurred and "no reaction of the galvanic response was observed." Since other clinicians have previously ignored changes in response to repeated stimulation as great as 50 to 100 per cent (cf. 62), Huizinga's failure to note habituation to galvanic stimulation must be interpreted with extreme caution.

King, 1926 (51) studied the influence of repeated rotations on decerebrate and on blinded squabs. Blindness was produced in other squabs by injection of chromic acid into the eyeballs. The rotation device employed "attained its maximum speed, 20 revolutions in 36 seconds, at the beginning of the second revolution . . . . and came to rest between 180 and 185 degrees from the point of initial deceleration." By fastening the bird in a specially prepared holder the nystagmic responses in the horizontal plane could be recorded for each animal. Some birds were rotated with the head free, others with the head fixed. King summarized his findings as follows:

> Responses to rotation showed only small decrease after seven days practice with head free; a much greater modification for same period with head fixed. The habituation to rotation-nystagmus is quantitatively the same in decerebrate and in normal animals, but the after-nystagmus suffers less reduction in decerebrate than in normal animals.
>
> Blind birds give less rotation-nystagmus and more after-nystagmus than do normal birds.
>
> Repeated rotation of blind birds causes a greater modification of the rotation-nystagmus than of the after-nystagmus.

Repeated rotation causes a greater reduction of nystagmus in blind than in normal birds, but a lesser reduction of after-nystagmus in the blind birds.

The inhibitory effect of visual stimuli on after-nystagmus appears to depend upon the functioning of the cerebral hemispheres.

Habituation to rotation does not seem to be of the nature of a learning process.

Of particular interest to us at this point is the fact that the degree of habituation for peripherally blinded and for centrally blinded (decerebrate) squabs was found to be quantitatively similar. This fact led King to conclude that habituation "must be effected in the lower centers of the central nervous system or in the receptors." While King's findings neither support nor oppose a "central" interpretation of the habituation effect they serve to focus attention upon the cerebellum as the place most likely to harbor this process.

DEVELOPMENT OF RESPONSE TO ROTATION

Although there has been no dearth of theories concerning the nature of the habituation process (see below) there has been almost a minimum of experimentation concerning the development of the response which later becomes modified by repeated elicitations. Since it has become increasingly apparent in recent years that before there can be a complete description of the process whereby a response may be modified it is necessary to know the history of the processes by which the response was acquired, this deficiency is a considerable one. Two studies, one of which is not available in published form, have been reported concerning the development of responses to rotation.

Stoltenberg and Fearing, 1929 (80) in a paper presented to the International Congress of Psychology reported their observations of early responses to rotation in squabs. Birds aged 5, 10, 20, 35, and 90–120 days were rotated 5 times in alternate directions on 10 successive trials. A trial consisted of 10 turns in 20 seconds with an interpolated rest period of about 2 minutes. Each age group consisted of from 14 to 16 birds. Both the number of head movements and the duration in seconds of nystagmus were noted. From a summary of these data recently reviewed by Stone (81):

> It may be noted that up to 35 days, the approximate time at which squabs leave the nests, there is an age increase in both the number of movements and the duration of time during which they were made. Also, excepting the 5 day-old birds, in which little change was observed there is a decrease (habituation) in the frequency and duration of the movements.

The following table reproduced from Stone's paper indicates the degree to which the various age groups became habituated by ten successive elicitations of nystagmus.

Average of the time intervals in which post-rotational nystagmic movements were observed in different age groups of squabs

(After Stone)

ROTATIONS	5-DAY	10-DAY	20-DAY	35-DAY	90–120-DAY
1 and 2	3.66	10.75	19.11	23.59	23.56
9 and 10	3.67	8.07	13.68	16.20	17.13
Decrease.....	−0.01	2.68	5.43	7.39	6.43
Percentage decrease...	−0.27	25.80	28.40	31.40	27.30

Fish and Windle, 1932 (27) observed the movements of the head and eyes in new-born and in young kittens in response to rotatory stimulation. It was found that vestibular nystagmus both during and following rotation appeared in 75 per cent of the five to seven day-old kittens whose eyes had been opened surgically. Deviations and irregular oscillations of the eyes were observed from one to two days before a true nystagmus appeared in response to rotation. In the very young kittens the nystagmic movements were slow and followed an appreciable latent period, but by the end of the third week responses characteristic of the adult were found.

Substantial agreement is to be noted in the two foregoing studies with reference to certain important particulars: response to rotation is but little (if at all) developed at birth; it undergoes rapid development during the three to five weeks subsequent to birth at the end of which time responses characteristic of the adult are found.

THEORIES CONCERNING THE NATURE OF THE HABITUATION PROCESS

Four theories have variously been offered to account for the phenomena of habituation: (1) peripheral theory, (2) "fatigue" theory, (3) central modification theory, and (4) habituation as "learning" theory.

Peripheral theory. This theory holds that habituation is based upon a structural alteration of the end-organ (labyrinth) associated with successive and prolonged rotation. The limited evidence in support of this theory was reviewed above: (see Breuer 8, Huizinga 48, and Steinhausen 79).

"Fatigue" theory. This theory regards the disappearance or habituation of response to rotation as the result of "fatiguing" the response by repeated elicitations. The theory was proposed by Hoshino, 1922 (45) who subjected rabbits to a single period of successive rotations and thereby reduced their nystagmus times. After a few hours of rest Hoshino again tested the rabbits and noted a considerable degree of "recovery" from the habituation effect similar to the recovery which a man shows after resting following vigorous exercise. Mowrer (62) has criticized the "fatigue" theory on the grounds that recovery was probably not complete and that the effects of one session would have summated with the effects of subsequent sessions. Evidence has been reviewed above and additional evidence has been obtained in the present investigation which indicates that some effect of habituation can be detected as long as several months after the end of the habituation period, a fact which is incompatible with a "fatigue" interpretation (cf. Griffith 35, and Dunlap 18).

The *"fatigue" theory* invokes a singularly weak analogy as an explanatory principle. While it is true that "fatigue" and habituation are both characterized by decrement of response, under physiological conditions the former is further characterized by complete reversibility whereas the latter is not. Thus Griffith (35) and others have noted that following a considerable lapse of time, habituation was re-established at a faster rate than in the original instance. Still another factor serves to differentiate the phenomena of habituation from those usually connoted by the term "fatigue." Within limits the "fatigue" process is completely reversible, but beyond a critical point the end-point of "fatigue" is *pathology*. In other words, "fatigue" may proceed to a point where actual breakdown of structure occurs. The end-point of habituation, on the other hand, is a physiological plateau without any known structural disintegration as the basis. The comparative summary below reveals the marked inadequacy of the *"fatigue" theory*.

CHARACTERISTIC	"FATIGUE" PROCESS	HABITUATION PROCESS
Decrement of response	Yes	Yes
Complete reversibility (within limits)	Yes	No
End-point (beyond critical limit)	Pathology	Physiological plateau
"Recovery" phase (i.e., loss of effect)	Rapid (minutes or hours)	Slow (weeks or months)

Central modification theory. In contrast to the *peripheral theory* this theory holds that the processes whereby nystagmus is sustained for a relatively long period after cessation of peripheral excitation occur within the central nervous system. Lorente De Nó, 1933 (57) is a proponent of this theory. According to him:

> Nystagmus is nothing else than an alternating reflex similar to other known rhythmic reflexes. The peripheral labyrinthine stimulation sets into activity a machinery which gives rise to nystagmus in the same way as the spinal cord sets up the scratch reflex as a response to a stimulus produced on the skin.

De Nó has postulated an elaborate system of "self-reexciting neurone chains" which he holds are capable of rhythmic action and which therefore may set up a prolonged after-discharge. Ingenious as such a scheme may be neurologically speaking, it is scarcely adequate to account for all of the phenomena now known to be associated with the habituation process. Limited evidence for post-natal development of response to rotation is available (see discussion elsewhere). In one instance it is of such character as to suggest strongly processes in which "learning" plays an important rôle. Thus it is indeed courageous to stress, as De Nó does, the mechanical aspects of the nystagmic response.

It is possible of course that if not identical at least somewhat similar processes to those postulated by De Nó (suggested earlier by Bárány and by Ranson and Hinsey) constitute the structural basis for the changes which the psychologist terms "learning." So far, attempts to relate the two have uniformly resulted in failure. Until such intimate relationship has been established beyond question, the psychologist must continue to use the term "learning" to imply *functional* modification of the organism.

Habituation as "learning" theory. This theory, first formulated by Abels, 1906 (1), holds that habituation is a process whereby a "useless type of response" (i.e., useless under usual conditions for elicitation) is eliminated, and hence it is similar to other processes frequently termed "learning." Dodge (16) and Mowrer (62) have variously supported this interpretation. The former wrote in 1923:

> This disappearance of the reflex in protracted rotation is on several counts an interesting adaptation. Unless the ocular compensation is useful it simply dies out. Why not? . . . . According to our scientific tradition the two processes are direct opposites. In ordinary learning some discreet reaction is gradually established and consolidated. In our habituation experiments a reflex gradually enters a pronounced refractory phase and is temporarily disestablished.

The writer elsewhere in this monograph develops the thesis that the phenomena of habituation are essentially similar to those conventionally designated as "learning." But he seriously questions the efficacy of the use of such a phrase as "useless type of response" in connection with habituation. It is extremely doubtful whether any response is ever "useless." Unless one is to postulate some generalized principle of *least action*, evidence for which is exceedingly ambiguous (Klüver, 1933, 51a), it is clear that such usage soon becomes meaningless.

Other investigators have noted certain similarities between habituation and "learning" phenomena (cf. Griffith 34, Fearing 20, and Razran 68). Razran believes that the phenomena of habituation support his theory of *Asynchronization*. We shall not discuss his theory at this point other than to indicate that it attempts to account for the processes whereby reflexes, especially "conditioned," become extinguished.

SUMMARY OF CEREBELLAR-CEREBRAL RELATIONSHIPS

In addition to anatomical and phylogenetic evidence (which need not be reviewed here) there are a few studies which indicate a close functional relationship between the cerebellum and the cerebrum. For purposes of subsequent reference we have summarized the various findings below.

Bremer, 1922 (6) has shown that electrical stimulation of the cerebellar cortex inhibits decerebrate rigidity.

Rizzolo, 1930 (70) found that electrical stimulation of a lateral lobe of the cerebellum increases the excitability of the cerebral cortex, chiefly of the contra-lateral side.

Fulton, 1932 (29) observed that the tremor "characteristic of a decerebellate animal" does not appear if the cerebrum has also been removed.

Adrian, 1935 (2) reported that both the cerebellum and the cerebrum exhibit a phenomenon not observed in peripheral structures, viz., a continuous play of spontaneous electrical activity. While the frequencies of these potential changes are quantitatively different for the two structures, activity in the cerebellum proceeding at a rate three or four times that of the activity in the cerebrum, their simultaneous occurrence renders functional relationship extremely probable.

Lashley and McCarthy, 1926 (54) studied the survival of the maze habit in white rats after cerebellar injuries (cauterization). They concluded that "there is no evidence that the cerebellum plays any part in the performance of the maze habit." A criticism of the evidence upon which this conclusion was based is made elsewhere.

BEHAVIOR FOLLOWING CEREBELLAR DESTRUCTION

Flourens, 1842 (28), Hoshino, 1919 (44), Bremer and Ley, 1927 (7) and Groebbels, 1928 (36) have observed the behavior associated with cerebellar injuries in birds. A subsequent section of this report deals with similar observations made in the course of the present investigation and contains a summary of the studies indicated above.

CHAPTER III

General Statement of Procedures

As stated in the introductory chapter, the present investigation is an attempt to determine the effects of cerebellar lesions upon the phenomena, commonly designated as habituation, which result from repeated elicitation of post-rotational nystagmus. In this report data relating to rate of habituation, retention of habituation (especially subsequent to lesion) and variability in response receive particular attention. In addition, limited data are reported with reference to re-establishment of habituation after impairment by lesion, latency changes associated with habituation and transfer of habituation.

Approximately 80 adult common pigeons (*Columba domestica*) were employed. Of this number detailed records are reported for 60. These latter were divided into three groups of 20 birds each. The three groups are hereafter referred to as Experiment I, Experiment II (A), and Experiment II (B) respectively. The purpose of Experiment I was to determine whether birds with cerebellar lesions would habituate as readily as normal birds during a ten-day period in which post-rotational nystagmus was repeatedly elicited. Accordingly, the birds used in this experiment were of two types: (1) ten birds which from four months to one year prior to any rotational test had received the same type of cerebellar lesions, (2) ten normal (unselected) birds which served as controls.

Experiment II (A) was designed to reveal the effects of a cerebellar lesion acquired *after* habituation to rotation had been established. Twenty normal birds were habituated in the regular manner. These were then divided into two groups, of ten birds each, equated as to the average amount of habituation that had resulted from the practice period. The birds in one group were subjected to a standardized cerebellar operation and two weeks later were tested for retention of habituation; the other group (controls) received no operation but after two weeks were also tested for retention.

This same procedure was repeated with the twenty birds in Experiment II (B) except that following the end of the practice period the critical test for retention was made four weeks later. Thus these two groups of animals (ten birds each) were habituated in the same degree; the members of the first group, however, received a cerebellar lesion and four weeks later were tested for retention; the members of the second group (controls) received no lesion but also were tested for retention after a four week interim.

OPERATIVE PROCEDURES

a. The pigeon as an experimental animal

Several factors combine to make the pigeon a very desirable animal for use in investigations such as the present. Availability, ease of handling and of maintenance, long history of domestication, resistance to disease and infection are some of the favorable considerations. For purposes of brain operations the bird is singularly well adapted. Aseptic methods are not necessary (no case of infection was encountered in this investigation). Surgical anaesthesia may readily be induced by methods described below. Recovery from the immediate effects of an operation is usually rapid providing gastric disturbances do not develop. Even in the latter event the amount of nursing required is small.

The cerebellum is relatively speaking the most highly developed structure of the avian brain. Taken as a whole it is homologous with the vermis of the mammalian cerebellum. As indicated previously relatively little is known concerning its physiology. For surface lesions the avian cerebellum is not well adapted. The prominent dorso-median sinus, the location of the superior vestibular canals and the jugular sinus covering the caudal surface combine to render eighty per cent of the outer surface of the cerebellum inaccessible for purposes of circumscribed lesions. A satisfactory technique for placing deep lesions in this structure was developed, however, and is described below.

Operation

The rectal temperature of the bird was obtained then its weight was recorded. Feathers were removed from top of head and well down the neck of the bird. An injection of a sterile solution of Nembutal[2] proportionate to the weight of the animal was then made into the muscles surrounding the sternum. A state of surgical anaesthesia usually followed within ten or fifteen minutes after injection. In case of exceptions ether was used to supplement the injection.

The skin over the cerebellum was opened with a single midline incision approximately one centimeter in length. Outline of the dorso-median sinus could be made out through the soft spongy bone of the skull which had thus been laid bare. Orientation between the sinus and the region known to cover the superior canal was next established for purposes of opening the skull without damage to either of these structures. A $\frac{1}{8}$-inch opening was next made bilaterally over the retro-lateral surface of the cerebellum by means of a machinist drill manipulated in the fingers. The blunt nose of the drill prevented untimely entrance into the dura which was frequently exposed without rupture of any of its peripheral vessels. (The location of the major peripheral vessels had previously been established by the study of two gelatin mass injection specimens prepared for this purpose by the writer.)

With the wounds cleared a thermo-cautery made of 22 gauge nichrome wire (heated by means of an AC doorbell circuit) and heated to a near white intensity was passed through the mass of the cerebellum by a standardized movement in each of three planes: lateral, caudal, and ventral respectively. In each case these motions were performed bilaterally.

In roughly 90 per cent of the cases no hemorrhage was encountered and the skin wound was closed immediately either by silk stitches or by means of silver wound clips. When hemorrhage did develop (in each instance brisk but readily controlled) the skin wound was not permanently closed at once. Healing in every case was rapid.

The time required to perform the operation ranged from ninety minutes in the beginning to twenty-five minutes towards the last with an average of approximately thirty-five minutes. For protocols concerning behavior associated with the operation see Chapter IV.

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[2] A sterile solution of Nembutal is prepared by the Abbot Laboratories in Chicago which recommends 1 cc. per 2268 grams (5 pounds) of animal weight. Satisfactory results were obtained by this ratio injected intra-muscularly as indicated above.

ELICITATION OF NYSTAGMUS

The term *test* as used herein implies a series of observations, made under carefully standardized conditions, of the duration of post-rotational nystagmus on ten successive instances of elicitation. The term *practice* implies a period of successive elicitations of such nystagmus under equivalent conditions but for which nystagmus times were not recorded.

The rotator

This consisted of a vertical 2- by 30-inch shaft, mounted on bearings in a metal frame, secondarily driven (via worm gear) by a 1/2 HP D.C. motor connected by a belt and pulleys. On the upper end of the vertical shaft was mounted a tier of five wooden cradles each of which was designed to accommodate (and restrain) a pigeon (cf. Mowrer, 62). A small ½-inch shaft with a bearing stabilized the thrust of the unit during rotation. Starting and stopping was controlled by means of a double throw switch connected with the motor in such manner as to reverse the polarity of the field coils when opened. This "braking" device gave a stable curve for angular deceleration, the slope of which was determined empirically and found to change at the rate of 20.8 radians per second under the conditions employed.

During the habituation period each bird was given ten periods of rotation on each successive day for either ten or fourteen days. A rotation period consisted of 20 turns in 30 seconds. All rotations were in the clockwise direction (with an exception noted elsewhere) with a two-minute rest period between successive rotation periods. On days when nystagmus times were obtained birds were rotated individually; otherwise they were rotated in groups of five. The order of hooding, wrapping, and position in the tier was varied systematically throughout the practice period. With little exception room temperature was held at 70 degrees F. during rotation. Conditions of humidity, room illumination, olfactory and noise factors were reasonably constant from day to day. In every instance birds were rotated with vision excluded, this being affected by means of a chamois skin hood which covered the head.

Observation of nystagmus was made directly by the experimenter who timed the phenomena by means of a new split-second stop watch. By examining comparable data secured by different investigators in this laboratory, working with groups of unselected pigeons, it has been found that this procedure is highly reliable. In line with the experience of other investigators both in this and in other laboratories is the fact that in each case normal birds averaged 50 to 60 per cent habituation at the end of the practice period employed in the present investigation.

STATISTICAL PROCEDURES

Measure of habituation

In selecting a criterion of habituation the following factors were considered: (1) the unit of measure must be reliable; (2) it must be small enough to reveal the effects looked for over successive periods of time. The device which best satisfied these conditions and which is implied wherever the term *habituation* appears in the account of the present investigation is based upon the average of the ten nystagmus times secured for each bird on a given day. In every instance the first test day marked the beginning of a practice period which was terminated several days later by a second test day. By comparing the performance on each of the test days a measure of habituation was obtained according to the following formula:

$$H = 100 - \frac{M_2}{M_1}$$

where H equals habituation, M_1 equals the mean nystagmus time for test I, and M_2 equals mean nystagmus time for test II.

Such a measure was found to differentiate statistically between the performances on successive test days for the same group as well as between comparable test days for different groups.

Measure of retention

In order to determine something about the permanency of the habituation effect a measure of retention was required. A simple and relative measure of retention was obtained by the formula:

$$R = \frac{M_2}{M_3}$$

where R equals retention, M_2 equals mean nystagmus time on test II, and M_3 equals mean nystagmus time on test III.

The data from which the various statistical constants were computed are on file in the laboratory of Prof. Franklin Fearing, Northwestern University. In preparing the various tables in their present form constants are employed based upon unrounded data; slight discrepancies thus introduced in summating in general invade only the second place to the right of the decimal point.

CHAPTER IV

BEHAVIOR FOLLOWING CEREBELLAR DESTRUCTION

The classic description of the behavior changes which accompany cerebellar lesions is that made by Pierre Flourens in 1842, based upon pigeons. So great was the prestige of Flourens in his time that his researches are still the subject for reference in many text-books of neurology and physiology. Perhaps most widely quoted is the work which he did on cerebellar functions. A translation of his original account of this research as published in 1842 (28, p. 38) is offered below.

> I removed *successive layers of the cerebellum*[3] of a pigeon. During the ablation of the first layers, only a slight weakness and lack of harmony of movement appeared.
>
> Removal of the middle layers was followed by the appearance of a generalized tremor; movements became brusk and irregular. Hearing and sight remained.
>
> Upon removal of the last layers, the animal, of which the abilities to jump, fly, walk, and hold itself still had been more and more impaired by the preceding mutilations, completely lost these abilities.
>
> Placed upon its back it was not able to right itself (il ne savait plus à relever). Far from remaining calm and poised as in the case of pigeons deprived of the cerebral lobes, it thrashed about recklessly and almost continuously, but it moved in a direct or determined manner.
>
> For example, it could see a menacing blow and would try to escape—would make a thousand contortions in an effort to escape—but could not do so. Placed upon its back it did not wish to remain there, made vain efforts to right itself, and ended by remaining there in spite of itself.
>
> Finally, volition, sensation and perception persisted, as did the capacity to execute movements together; but the coördination of these movements, as in the regular fixed motions of locomotion, was lost.

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[3] Italics mine.

It should be noted that Flourens worked without anaesthetics and without knowledge of the cytoarchitecture of the structures with which he was dealing.[4]

Just what Flourens meant when he said that he *removed successive layers of the cerebellum* is not clear. Presumably the reference is to the natural layers or folia of the cerebellum. In any event the probability is great that the phenomena which he described were contributed in some part by damage done inadvertently to underlying vestibular structures. Thus there is little wonder that Flourens concluded that cerebellar symptoms are nearly identical with those produced by destruction of the non-acoustic labyrinths.

Finally, concerning cerebellar functions, Flourens' observations were confined to acute preparations (animals freshly operated) a fact which according to Von Monokow's theory of diaschisis vitiates their significance.

Lashley (55) has summarized the theory of diaschisis as follows:

> 1. Destruction of a (cortical) area may result in symptoms which are due to the withdrawal of facilitation from some other area and the resultant inadequacy of functioning of that facilitated area. 2. Areas subject to such diaschisis effects recover their functions spontaneously, but no limit can be set to the time required for such recovery. 3. Only such functions as are permanently impaired can be ascribed to a destroyed area.

Since Flourens, many studies have been reported which have been concerned with variously alleged functions of the cerebellum in the bird and particularly in mammals. That little of positive significance has resulted from these studies is reflected in Magnus' statement quoted in our Introduction (58). For this reason no attempt is made to review this extensive literature at this time. We pass instead to a consideration of some observations made on pigeons with cerebellar deficiency which had not, however, resulted from surgical interference.

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[4] During his productive years, 1820–1865, the uses of techniques of histology were little known (thus, Rolando in 1824 first cut thin sections of chemically hardened brain tissue; Stilling in 1842 developed a method for cutting serial sections so that structures might be traced beyond the plane of the section; and Gerlach in 1858 discovered the use of carmine in staining neurological tissue.

Hoshino, 1919 (44) analyzed the brains and spinal cords of a family of pigeons with hereditary ataxia. Seven pigeons, four ataxic and three normal, all from the same strain, were observed for behavior symptoms over a period of three months. Since the analysis revealed cerebellar involvement in the affected birds it is of interest to review this paper somewhat in detail. The ataxic strain first developed incidentally in connection with Riddle's investigations on "reproductive overwork" (1918) and is extant.

A study reported by Koch and Riddle, 1919 (52) closely parallels that of Hoshino except that the former were interested in the chemical composition of the brains of ataxic and normal pigeons. Concerning the relationship between the respective findings, Koch and Riddle stated:

> Although the present study was completed and fully described before we were aware of Hoshino's results, it seems well to add here that the neurological and chemical studies support an essentially similar view. The bearing of Hoshino's summary statement is self-explanatory: "This (the changes in the central nervous system in the affected pigeons) may be regarded as a hypoplasia or developmental inhibition in the proprioceptive system, part of the motor system, and some structures connecting the medulla oblongata and cerebellum, occurring during growth, with scarcely any definite degeneration or secondary increase of neuroglia tissue."

Hoshino gave a fairly detailed description of the general picture of impairment presented by the ataxic pigeons. For purposes of subsequent reference it is reproduced here.

> The affected birds apparently are backward in their development, they look smaller, their feathers are scanty; they have lost the characteristic brilliant color, and appear lusterless. The muscles are flabby. The birds maintain one position quietly and almost constantly. To support the body they stretch their legs wide apart and a little forward with the tail braced against the bottom of the cage and the trunk partly lowered to the floor, so as to avoid falling forward, backward or to the side. The pigeons, then, maintain their position while standing with

three supports just like a three-legged stool; two widely spread legs and a tail braced against the floor. The affected birds do not stand on the limb of a tree as normal pigeons usually like to do, but remain on the floor of the cage, often supporting themselves on one side of the body with the wall of the pen. If food or water is placed in the middle of the cage on the floor, they have great difficulty in reaching it. Food is really the only thing which will make them attempt to walk, except when they are frightened or excited. In their attempts to walk they fall forward or sideways or just stumble along reeling like a drunken man, "demarche ebrieuse." When they fall forward they try to get up with their bills against the floor pushing back the body and flapping the wings with much effort. When they fall to the side they usually roll over once or twice. Sometimes they fall to the right, while at other times they fall to the left and then roll until they reach some obstruction which helps them to get up with the aid of flapping the wings. Flying is practically impossible in all birds; if they are thrown free in the air, they flap their wings irregularly and cannot fly above the height they are thrown, but go directly down to the floor notwithstanding that their flapping efforts are much more intense than those of normal birds. When the birds are excited or frightened, the disturbances of the irregular movements stated above are much more apparent. Such a movement as the so-called "tremulance" or oscillatory movements cannot be observed either when the birds are excited or at rest. Ocular movements are free, no deviation and no nystagmoid jerking can be substantiated. The reflexes which may be elicited from the cornea are normal. *When they are put on a rotating chair they show the head nystagmus characteristic of normal pigeons.*[5] If they are rotated more than five or six times they lean against the cage wall or lie down, exhibiting regular head nystagmus. When blindfolded the birds reveal no increase of the disturbances of coördination.

As far as can be determined, sight and hearing are normal; the birds can recognize food and an observer who may be approaching; they also react to a sudden sound by raising the head and trunk suddenly, but immediately lower them again. Pupils are equal and react to light promptly. The sensibility to touch as well as to pain appears unaffected in the skin; the birds react to stimulation with direct movements, but these movements are quite sluggish. The toes of three affected pigeons are more or less flexed and widely abducted, so that the web spaces appear quite large and toes show so-called hollow-foot. They do not

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[5] Italics mine.

"coo" or make any other noise. To observe the intelligence of a bird is of course always difficult. So far as we can see from the behavior of the birds, the intelligence seems not to be far different from that of the healthy birds; they show movements of uneasiness and fear, if one approaches them or tries to catch them they begin to move away as one approaches. They distinguish food from uneatable objects, and show a preference for the place in the cage where the body is most conveniently supported.

No bird shows a limitation to a particular kind of incoördinated movement;[6] all of them have a nodding head and neck and even a swaying trunk, tipping forward and backward and falling to either side. The unsteady staggering gait, tipping head, and swaying trunk are the common symptoms in all effected birds with of course variations in degree. A weakness of the sphincter of rectum or bladder cannot be detected in any bird.

Bremer and Ley, 1927 (7) and Groebbels, 1928 (36) have investigated the physiology of the avian cerebellum; in both instances the data were obtained under conditions sufficient to render them of dubious significance.

OBSERVATIONS MADE DURING THE PRESENT INVESTIGATION

As a part of the present investigation birds which received a cerebellar lesion were systematically observed during their post-operative period of re-constitution (i.e., the period during which pre-operative behavior patterns re-appear). These observations consisted of a ten-minute sample of the bird's behavior while in a standard environment, secured on successive days and in general at the same hour of the day.

The observatory

This consisted of a small room 4 by 4 by 3 feet in size which was constructed in the laboratory. Two 60 watt lights gave an interior illumination sufficient to exclude visual stimuli from the outside arriving by way of the 4- by 8-inch glass observation window. A wire partition made it possible to observe an operated and a control animal at the same time. A door-bell and a moveable stick, both of which were controllable from the outside, were mounted in the interior.

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[6] Italics mine.

In making the observations a check-list of symptoms, developed by Fearing in connection with his work on labyrinthine functions, was employed. The symptoms to which the check-list corresponded are briefly described below. The symbols used in the check-list appear at the left; the legend for each is given at the right.

Feeding and drinking responses

Artificial feeding.	Notation of number of grams of food and cubic centimeters of water which were force-fed.
Feeding.	Check if bird observed eating or drinking.

Body position

"B"	Slant of the body to either direction, bird keeping both feet on the ground. (Indicate direction.)
"H"	Slant of the head to either side; not more than 90 degrees deviation from the vertical. (Indicate direction.)
"LW"	Legs more widespread than normal, feet usually show tendency to slide laterally with any voluntary body movement.
"LE"	Abnormal extension of legs.
"LF"	Abnormal flexion of legs.
"O"	Normal standing position. "B" and "H" may be present (indicated elsewhere on sheet), but there is no torsion or head curl; weight is supported by feet alone. (See other positions.)
"I"	Body erect, weight on both feet, torsion of the head to right or left beyond a 90 degree deviation, usually 180 degrees or more, so that back of head is directed toward ground, but not touching it. (Indicate direction of torsion.)
"II"	Torsion of head to right or left beyond a 90 degree deviation, usually 180 degrees or more, back of head, one shoulder and both feet on ground. Legs usually flexed. (Indicate direction of torsion.)
"III"	Torsion of head to right or left beyond a 90 degree deviation, usually 180 degrees or more; body vertical, legs extended, weight supported on back of head. This position is terminated in most cases by a somersault. (Indicate direction of torsion.)

“IV”	Torsion of the head to right or left beyond a 90 degree deviation, usually 180 degrees or more, weight on side of body and head, feet completely off floor. (Indicate direction of torsion.)
“V”	Both feet on floor, head curled or rotated 180 degrees or more about the bi-temporal axis. Back of head usually resting on floor.

Movement symptoms

“W_1”	Walks spontaneously.
“W_2”	Walks slowly.
“W_3”	Walks forward.
“W_4”	Runs.
“Pm”	Bird makes peering movements when walking.
“HO”	Bird walks with head outstretched.
“C”	Circling or “circus” movements. Rotation of the bird about its vertical axis continuing for 360 degrees or more.
“MT”	Movement of torsion. This includes the movement to the position of the head described in positions II or IV and the movement of recovery to the erect position as well. The total movement is quick and jerky. The bird may hit the floor violently with its head or not touch it at all. (Indicate position of torsion.)
“CHM”	Circular head movements. Movement of rotation of the head about the longitudinal axis through 360 degrees or more.
“EHR”	Erratic head movements. Uncontrolled voluntary head movements.
“PHM”	Pendular head movements. Movement of the head about the vertical axis from one side to the other through approximately 180 degrees.
“S”	Somersault.
“F”	Forced movements. Bird lies on one side, twists head, and extends and flexes wings, legs, and claws convulsively.
“M”	Backing. After twisting or curling the head, the bird moves its body backwards in short sharp jerks. (Indicate whether accompanied by torsion or head curl.)
“R”	Rolling about the various body axes. May or may not be accompanied by convulsive flexion and extension of wings, legs, and claws.

"HT"	Head tremor.
"V"	Veering; the bird swings in an arc to the right or left during forward progression.
"Q"	Staggering to right or left during forward progression.

Flight symptoms

"A"	Pitching; the bird falls heavily to the ground, breaking fall somewhat by extending (*not* beating) wings, and landing on feet.
"D"	Swerving; flight almost normal, but instead of flying in a straight line or a curve in a constant direction, irregular and erratic dips and curves appear.
"E"	Spiraling; the bird rotates in the air, about its vertical or longitudinal axis. This symbol also includes flying backwards; the longitudinal axis is almost perpendicular to the ground and the bird moves backwards, beating wings rapidly.
"N"	No flight; if tossed into the air or after spontaneous taking off from the ground, the bird falls heavily without breaking fall and lands in any position except on feet.
"Normal"	Flight resembles that of normal birds.

For use with cerebellar animals two additional symptoms were added to the foregoing list:

"SL"	Sluggishness. Bird is in general "non-reactive." Bird retreats to a side wall or back of the observation cage where it remains (sometimes for support but not always) in spite of intense prodding.
"SK"	Skating gait. In walking the bird takes unusually long steps which deviate from the plane of progression. These deviations fall within an arc of 30 degrees.

Condensed protocols for ten birds which received cerebellar lesions and were used in Experiment I of the present investigation are given below.[7] The protocols were prepared from the observation blanks filled out at the time of each observation period. In general, the observations were made daily during the first two weeks following the operation and then at irregular intervals over a period of four months.

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[7] The lesions induced in birds of Experiment II (A) and (B) were less extensive than those described in the protocols below. The period for re-constitution was shortened also. Every bird was able to eat and fly "normally" within six days following the cerebellar operation. (See page 74.)

Bird G36

11/ 5/33 Normal bird. Sex undetermined.

11/ 6/33 8:15 P.M. Nembutal anaesthesia. Fifty-five per cent cerebellar lesion induced by cautery. Almost no hemorrhage. Spontaneous nystagmus appeared after first entrance of cautery. Opisthotonoid posture (concave arching of tail and neck) upon awakening. Temperature dropped from 106.4 to 102.0°F. during operation. 10:00 P.M. Animal quiet. Opisthotonus and spontaneous nystagmus present. Placed in cage for night.

11/ 7/33 Temperature 102.0°F. No body symptoms present; no movement symptoms; flight normal. Bird very excitable, and walks continuously about the observation cage. At sound of bell bird stood on left leg and attended.

11/ 9/33 Temperature 103.2°F. No body symptoms and flight normal. Staggers when walking. Also over-stepping or skating gait.

11/11/33 Temperature 102.7°F. Animal force fed and watered. Pronounced body and head slant to right. Legs extended and widespread. Some erratic head movements and two instances of violent forced movements. Bird walks slowly (forward) and staggers.

11/12/33 Temperature 104.4°F. Animal force fed and watered. Symptom picture same but more marked in each instance except that no forced movements appeared.

11/13/33 to 11/27/33 Temperature and weight had returned to pre-operative level. All body and movement symptoms with exception of skating gait had disappeared; flight normal. No recurrence.

1/ 5/35 Post mortem revealed no evidence of extra-cerebellar involvement.

Bird G68

12/26/33 Normal bird. Male.

12/27/33 2:30 P.M. Nembutal anaesthesia. Fifty-two per cent cerebellar lesion induced by cautery. Brisk hemorrhage developed which was controlled with difficulty. Intense spontaneous nystagmus appeared and persisted after first insertion of cautery. Marked opisthotonus present before bird awakened. Temperature dropped from 108.0°F. to 107.0°F. during operation. 5:00 P.M. Opisthotonus gone; wings, neck, and legs flaccid. Spontaneous nystagmus persists. Three instances of forced movements. 9:00 P.M. Spontaneous nystagmus gone; animal quiet.

12/28/33 Temperature 107.5°F. Body and head slant to the right; left leg extended and both widespread. Bird walks slowly (forward) without peering movements. Marked erratic head movements and staggering. When placed with mate in observation cage bird showed aggressive behavior, uttering mating sounds. Made repeated but poorly coördinated efforts to repulse a second male introduced to the cage when the latter approached the female. Unable to fly.

12/29/33 Temperature 107.5°F. Leg positions same as preceding. Body and head slant uncertain. Staggers, walks slowly (will not run when prodded) without peering movements. No flight.

12/30/33 Temperature 106.0°F. Animal force fed and watered. Body and head symptoms again marked. Body and head slant to right. However, the right leg is now extended. Head torsion to the right (II) approximately 100 degrees. Erratic head movements and staggering persist; no flight; sluggish in reactions.

1/ 1/34 Temperature 106.6°F. Body slant to right; head slant to left; right leg extended; no head torsion. Generalized body tremor. Spontaneous nystagmus present when hooded. Other symptoms unchanged. Bird reacted to sound of bell.

1/ 3/34 Temperature 106.4°F. Body and head slant to the left now; but right leg is still extended. Peering movements present in progression; body tremor and staggering present. Bird flew normally when released.

1/12/34 Body and movement symptoms gone. No recurrence. Skating gait persists.

1/ 5/35 Post mortem revealed damage to vestibular ganglion on both sides. Chromatolyzed cells and empty capsules were found in both ganglia.

Bird 119

12/23/33 Normal bird. Male.

12/24/33 1:20 P.M. Nembutal anaesthesia. Eighty-four per cent cerebellar lesion induced by cautery. Lesion made on right side without difficulty. On left side mild hemorrhage developed which was readily controlled. Marked spontaneous nystagmus appeared after first insertion of cautery. No opisthotonus but a distinct torsion of the head to the right appeared before the animal awakened. 2:15 P.M. Animal awake and badly disturbed. Lies on left side with left leg extended and right leg flexed; head drawn to right. Feeble but distinct forced movements frequent. Temperature dropped from 108.0°F. to 106.0°F. during operation. 5:00 P.M. Animal quiet; spontaneous nystagmus still present.

12/25/33 Temperature 106.2°F. Body and head slant to right. Legs widespread with left leg extended. Head torsion to right. When placed in sling there is marked hypertonicity of the left leg with head torsion to the right. Upon hooding the bird the hypertonicity shifted to the right leg and head torsion changed to left. Spontaneous nystagmus present. No flight; no voluntary movement.

12/26/33 Temperature 106.0°F. Animal force fed and watered. Body and head slant to the right and left leg extended. Head torsion reduced. One instance of forced movement of brief duration. Bird flapped wings feebly when suspended in sling.

12/27/33 Temperature 104.0°F. Body symptoms unchanged. No voluntary movement. When prodded the bird is able to take a few poorly coördinated steps. Reacted sharply to sound of bell. No flight.

1/10/34 Temperature 107.4°F. Bird now flies normally. Head torsion gone; slight body and head slant to the right still observable. Mildly staggering gait. When suddenly released the bird runs across the floor of the cage and bumps against the wall.

1/14/34 Temperature 107.0°F. Legs widespread, otherwise no body symptoms. Voluntary movement appears well coördinated. Flight normal. Skating gait has persisted since operation. No recurrence.

1/ 5/35 Post mortem revealed no evidence of extra-cerebellar involvement.

Bird G52

12/25/33 Normal bird. Female.

12/26/33 2:45 P.M. Nembutal anaesthesia. 47 per cent cerebellar lesion induced by cautery. Brisk hemorrhage of brief duration on both sides. Marked spontaneous nystagmus followed first insertion of cautery. Opisthotonus appeared after the bird awakened. 5:30 P.M. Animal quiet. Opisthotonus and spontaneous nystagmus still present. Temperature dropped from 104.6°F. to 102.4°F. during the operation.

12/27/33 Temperature 105.5°F. Body and head slant to left. Legs widespread and right leg extended. No voluntary movement. Bird staggers when prodded into motion. No flight. Animal very sluggish in reactions.

12/28/33 Temperature 106.5°F. Bird was observed eating in cage. Body symptoms unchanged. Walks spontaneously but always slowly and without peering movements. No flight. Erratic head movements observed. When placed with mate is receptive to his uncoördinated advances (see G68) but fights awkwardly a strange male placed in the same cage.

12/29/33 Temperature 102.0°F. Body and head slant to left; legs widespread with the left leg now extended. Bird walks spontaneously but without peering movements and in a staggering manner. No flight. Bird very sluggish and uses tail as third point of support in standing.

12/30/33 Temperature 104.0°F. Animal force fed and watered. Symptom picture unchanged.

1/ 2/34 Temperature 106.0°F. Bird flies normally when released. Peering movements now present during walking. Symptom picture otherwise unchanged but is reduced in distinctness.

1/ 8/34 Temperature 107.6°F. Head and body symptoms gone. Flight normal. Bird still staggers slightly in walking. Skating gait has persisted through post-operative period. No definite recurrences.

1/ 5/35 Post mortem revealed no evidence of extra-cerebellar involvement.

Bird 179

12/21/33 Normal bird. Male.

12/22/33 1:30 P.M. Nembutal and ether anaesthesia. Thirty-three per cent cerebellar lesion induced by cautery. No hemorrhage. Spontaneous nystagmus present after first insertion of cautery. Opisthotonus appeared before bird awakened. 4:00 P.M. Animal quiet. Opisthotonus and spontaneous nystagmus still present. 5:00 P.M. Bird flew from desk to top of window in laboratory. Temperature dropped from 107.5°F. to 104.5°F. during operation.

12/23/33 Temperature 108.0°F. No body symptoms; no movement symptoms; flight normal.

12/24/33 Temperature 105.0°F. Body and head slant to right. Legs widespread and right leg extended. Walks spontaneously but staggers. Bird fails to react noticeably to bell. All reactions sluggish. Skating gait.

12/30/33 Temperature 107.5°F. Body and movement symptoms unchanged.

1/ 4/34 Temperature 107.0°F. No symptoms present. Bird very reactive to bell or prodding. No recurrence.

1/ 5/35 Post mortem revealed no evidence of extra-cerebellar involvement.

Bird 213

9/16/33 Normal bird. Male.

9/17/33 11:00 A.M. Nembutal anaesthesia. Fifty-eight per cent cerebellar lesion induced by cautery. Spontaneous nystagmus present after first entrance of cautery. No hemorrhage. No opisthotonus at any time. 2:30 P.M. Bird sits huddled on floor of cage. Successfully raised right leg and scratched back of neck. 9:30 P.M. No spontaneous nystagmus. When prodded bird ran across floor of cage and bumped into wall. Marked staggering or ataxia. No peering movements. Temperature dropped from 108.4°F. to 102.0°F. during operation.

9/18/33 Temperature 105.1°F. Bird observed eating in cage. Legs widespread, otherwise no body symptoms. Flight normal; gait staggering.

9/21/33 Temperature 108.2°F. Symptom picture unchanged. Bird has developed gastric disturbance.

9/23/33 Temperature 109.1°F. Gastric disturbance cleared up. Symptom picture unchanged.

9/26/33 Temperature 107.2°F. No symptoms present. No recurrence.

1/ 5/35 Post mortem revealed no evidence of extra-cerebellar involvement.

Bird 212

9/17/33 Normal bird. Female.

9/18/33 11:40 A.M. Nembutal anaesthesia. Thirty-one per cent cerebellar lesion induced by cautery. Spontaneous nystagmus present after first insertion of cautery. Cautery tip burned out and destruction completed on the left side by means of a small curved knife. No opisthotonus at any time. Temperature dropped from 107.0°F. to 101.6°F. during operation. 1:00 P.M. Bird left under heating lamp. Experimenter left laboratory and upon return two hours later bird was flying about room.

9/19/33 Temperature 107.6°F. Bird observed eating in cage. Legs widespread, otherwise no other body symptoms. Walks voluntarily but staggers. Flight normal. Fine body tremor present.

9/20/33 Temperature 107.1°F. Symptom picture unchanged.

9/22/33 Temperature 108.0°F. Marked body and head slant to left present. Otherwise symptom picture unchanged.

9/26/33 Temperature 106.1°F. Body and head slant reduced. Staggering and skating gait have persisted during post-operative period.

9/29/33 Temperature 107.2°F. No symptoms present. No recurrence. Skating gait no longer observable; bird appears perfectly normal.

1/ 5/35 Post mortem revealed no evidence of extra-cerebellar involvement.

Bird 215

9/17/33 Normal bird. Male.

9/18/33 9:00 P.M. Nembutal anaesthesia. Thirty-eight per cent cerebellar lesion induced by cautery. No spontaneous nystagmus appeared until a brief hemorrhage developed on left side. Opisthotonus appeared and lasted for 30 minutes. Temperature dropped from 107.0°F. to 101.9°F. during operation. 10:00 P.M. Bird quiet. Some spontaneous nystagmus still present.

9/19/33 Temperature 105.1°F. Bird observed eating in cage. Body and head slant to left. Legs widespread and right leg extended. Walks slowly (forward) without peering movements and in staggering manner. Flight normal.

9/20/33 Temperature 105.4°F. Symptom picture unchanged.

9/21/33 Temperature 106.1°F. Bird now makes peering movements when walking. Otherwise no change.

9/26/33 Temperature 106.8°F. No body movement or flight symptoms present. Bird appears perfectly normal. No recurrence.

1/ 5/35 Post mortem revealed no evidence of extra-cerebellar involvement.

Bird 223

9/16/33 Normal bird. Female.

9/17/33 10:20 P.M. Nembutal and ether anaesthesia. Forty per cent cerebellar lesion induced by cautery. Spontaneous nystagmus present after first insertion of cautery. No hemorrhage. Opisthotonus appeared before bird awakened. Temperature dropped from 108.2°F. to 100.4°F. during operation. 11:30 P.M. Animal quiet; spontaneous nystagmus and opisthotonus present.

9/18/33 Temperature 106.0°F. Body and head slant to right. Legs widespread and left leg extended. Bird walks slowly and spontaneously but without peering movements. Staggers in walking. Animal is sluggish in reactions and requires intense prodding to leave wall of cage. Flight is normal.

9/19/33 Temperature 106.7°F. Symptom picture unchanged.

9/21/33 Temperature 107.0°F. Legs widespread; otherwise no body symptoms present. Skating gait persists. Peering movements now present during walking. Bird very active; walks and flies voluntarily.

9/24/33 Temperature 107.0°F. Legs widespread; otherwise no body, movement or flight symptoms present. No recurrence.

1/ 5/35 Post mortem revealed no evidence of extra-cerebellar involvement.

Bird G63

12/24/33 Normal bird. Female.

12/25/33 4:40 P.M. Nembutal and ether anaesthesia. Thirty-seven per cent cerebellar lesion induced by cautery. No spontaneous nystagmus observed at any time. Marked opisthotonus appeared before bird awakened. No hemorrhage. Temperature dropped from 106.0°F. to 103.2°F. during operation. 7:00 P.M. Animal quiet. Opisthotonus gone. Temperature 104.2°F. Placed in cage for night.

12/26/33 Temperature 106.2°F. Body and head slant to left. Legs widespread and right leg extended. Bird walks spontaneously but very slowly. Peering movements are present. The gait is staggering. Flight normal. Bird reacts sharply to bell.

12/28/33 Temperature 107.5°F. Symptom picture unchanged.

12/30/33 Temperature 107.0°F. Bird observed eating and drinking. Body and head symptoms disappearing; otherwise no change.

1/ 7/34 Temperature 107.8°F. Legs slightly widespread; mildly staggering gait but otherwise normal bird in behavior. No definite recurrence.

1/ 5/35 Post mortem revealed no evidence of extra-cerebellar involvement.

INTERPRETATION OF PROTOCOLS

Detailed analysis of the temporal sequence of each of the various symptoms considered in the post-operative observations will be undertaken later. It is sufficient for present purposes simply to indicate the general course of the behavior changes associated with cerebellar lesions.

From the foregoing protocols it is possible to map this course in terms of three general periods.[8] The first we may term the *period of shock*. This period is characterized by severe postural disturbance, sluggish and poorly coordinated reactions and sometimes temporary loss of ability to fly. This period begins during the operation and may continue for from two to six days after the operation. The second period we may term the *period of re-constitution*. During this period a structurally modified organism regains functions which were temporarily lost following an operation. In regaining these functions the organism loses others which appeared associated with the *period of shock*. In the case of the birds reviewed here this period extends from about one to three weeks subsequent to the lesion. The modal time for complete re-constitution is apparently around two weeks of post-operative time. The third period we may term the *period of redintegration*. During this period the animal may exhibit many or all of the functions of a "normal" animal even though extensive structural modification has taken place.

The various periods just indicated are by no means mutually exclusive periods in the case of a particular cerebellar animal. For certain types of operations, for example, complete labyrinthectomies,[9] the *period of re-constitution* and the *period of redintegration* overlap greatly. Thus a bird which has shown considerable "recovery" from the more violent symptoms of totally

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[8] In treating the post-operative symptoms chronologically we have avoided the none the less interesting but somewhat more controversial question of the etiology of various symptoms. In connection with this latter two principle theories should be noted. The "*Reiz*" or *irritation* theory holds that symptoms which follow surgical interference are the result of stimulation on the side of the lesion; the "*Ausfall*" or *deficiency* theory holds that such symptoms are the result of stimulation on the side contralateral to the lesion. The two theories agree that unbalanced stimulation is the basis of symptoms; they differ concerning the relative position of the lesion in the total stimulation gradient, i.e., whether the lesion side is a high or low point. For a good summary of these theories particularly as they bear upon symptoms following labyrinthectomy in pigeons see Murray, 1933 (65).

[9] Writer's interpretation of one part of an extensive set of observation data made available through the courtesy of Prof. Franklin Fearing.

extirpated labyrinths six or eight months after the operation may suddenly exhibit a "re-constitution" of some of these violent symptoms. This in turn may be followed by a re-constitution of more "normal" behavior patterns. These phenomena of *symptom islands* (i.e., symptom patterns which appear associated in time with an immediately preceding and succeeding period of "normal" behavior) have been but little investigated. While such *islands* were not discovered during the observation of cerebellar birds, the probability appears great that more detailed and more frequently spaced observations made over a larger segment of the post-operative history would reveal them.

In striking contrast with the symptoms described by Flourens, which he regarded as characteristic (presumably permanently) of cerebellar deficiency, the present observations reveal a picture in every instance of almost complete re-constitution of "normal" behavior patterns within a period of less than four weeks. If we accept Von Monakow's dictum that "only such functions as are permanently impaired can be ascribed to a destroyed area," it becomes clear that Flourens never actually observed the behavior of a "cerebellar" animal. The present observations of post-operative symptoms are in line with the conclusion drawn by Magnus that:

> Unfortunately we know not a single function or reflex positively connected with the cerebellum. . . . . Our evidence of the postural activity of the cerebellum is purely negative (58).

In subsequent chapters experimental evidence is presented which indicates that under appropriate conditions the cerebellum functions directly in a "learning" situation.

CHAPTER V

HABITUATION OF BIRDS WITH CEREBELLAR LESIONS.

EXPERIMENT I

From this point it is convenient to consider the various parts of the general study as if each constituted a separately conceived experiment. In a later section (see p. 102) the findings for the various parts will be brought together for interpretation.

Selected upon the basis of relatively un-ambiguous post-operative behavior, ten birds (with cerebellar lesion) from a group previously described (see p. 37) along with the cage-mate (normal) of each as a control were habituated by means of repeated rotations. The nature and temporal sequence of these procedures were as follows:

Test I. Data consisted of ten readings per bird for duration in seconds of post-rotational nystagmus elicited by the method previously described (see p. 34). Birds employed had had no previous rotational experience in the laboratory.

Test II. Made on tenth day following Test I. Data and physical conditions similar to Test I. Birds had received rotational experience on nine successive days previously. While equivalent conditions were maintained throughout, readings were not made on eight of these days in the case of five operates and five controls.

Test III. Made two weeks after Test II. Data and physical conditions similar to Test I and II. However, birds had received no further rotational experience following Test II, and during this interim had lived under laboratory (cage) conditions. Following this test experimental animals were sacrificed immediately for preparation for post mortem analysis.

Unless specifically noted otherwise any subsequent reference to Test I, Test II, or Test III will imply the respective conditions indicated above.

The above procedure was designed to yield experimental results bearing upon such questions as the following: How do birds with cerebellar lesions compare with normal birds in

(1) Duration of post-rotational nystagmus when tested for the first time?
(2) The extent to which this initial duration is habituated (diminished) by successive periods of elicitation?
(3) The degree to which an habituation effect as in (2) is retained without re-inforcement (practice)?

What is the relationship between the extent of the lesion and the record for

(1) original duration?
(2) extent of habituation?
(3) degree of retention as indicated above?

Before considering the results for the various tests certain general and special factors should be noted or reviewed. The data summarized in table I were not all collected within one experimental period. Records of the first five operates and of the first five controls were secured in the spring months of 1934; records of the second five operates and controls were obtained during the early winter months of the same year. Cage temperatures probably did not vary at any time much more than plus or minus fifteen degrees from seventy degrees Fahrenheit. Room temperature under which observations were taken was held with little exception at seventy degrees plus or minus two degrees Fahrenheit.

Post mortem examination revealed damage to vestibular structures in the case of one bird (G68) of the ten considered below. Since for our purposes this bird represents an ambiguous preparation its record is not considered in computing the averages for the operated group. This record will receive individual consideration in another connection elsewhere in this report (see p. 99).

Evidence bearing on the first of the foregoing questions is to be found in the data of table I. Attention is called to the two sets of figures in the cross rows opposite Average. Those in the middle of the table represent the averages for the operated group; those at the bottom of the table are for the normal or control group. Differences between the group means for Test I, Test II, and Test III are arithmetically .2, 4.8, and 4.5 respectively.

What is the probability that these represent true differences? To answer this it is necessary to examine the reliability of each difference.

TABLE I

Showing habituation effect and retention of habituation effect in cerebellar and in normal animals (pigeons)

BIRD NUMBER	PER CENT LESION	MEAN TEST I	MEAN TEST II	MEAN TEST III	HABITUATION	RETENTION
Operates						
G36	55.0	10.0	9.0	11.0	10.0	81.6
G68*	52.0	48.9	25.6	31.6	47.7	81.0
119	83.6	16.9	9.3	11.5	45.0	80.7
G52	47.3	23.2	14.8	15.4	36.0	96.0
179	33.2	17.4	9.7	11.1	44.3	87.1
213	57.6	16.2	14.3	14.5	11.5	98.6
212	31.2	16.7	11.5	11.3	31.0	102.0
215	37.7	20.5	11.7	12.0	43.0	97.5
223	39.8	12.5	14.5	16.2	−16.0	89.4
G63	37.1	15.2	16.7	15.7	−10.0	106.0
Average . . .	47.0	16.5	12.4	13.2	21.6	93.8
Controls						
G49		10.4	4.8	7.4	54.0	64.8
G72		15.8	7.5	8.6	52.5	87.1
G38		15.7	4.0	4.3	74.6	93.0
G57		20.0	13.0	14.2	35.0	91.5
G78		19.0	6.6	8.6	65.3	76.8
286		16.5	8.1	8.9	51.0	91.0
279		17.9	7.9	8.6	56.0	92.0
283		18.9	9.0	10.6	52.4	84.7
291		18.9	7.3	6.8	61.5	107.0
298		13.9	7.8	9.2	44.0	85.0
Average . . .		16.7	7.6	8.7	54.6	87.4

* Data for this bird not included in averages for operated group (see p. 99).

THE CRITICAL RATIOS

A conventional check upon the reliability of the difference between two means such as the present is afforded by the ratio of a difference to its standard error, i.e., difference/sigma difference.[10] The left side of table II indicates the critical ratios and statistical constants involved in a comparison of the operated and control groups. The right side of this table gives similar information for the various measures taken within each group.

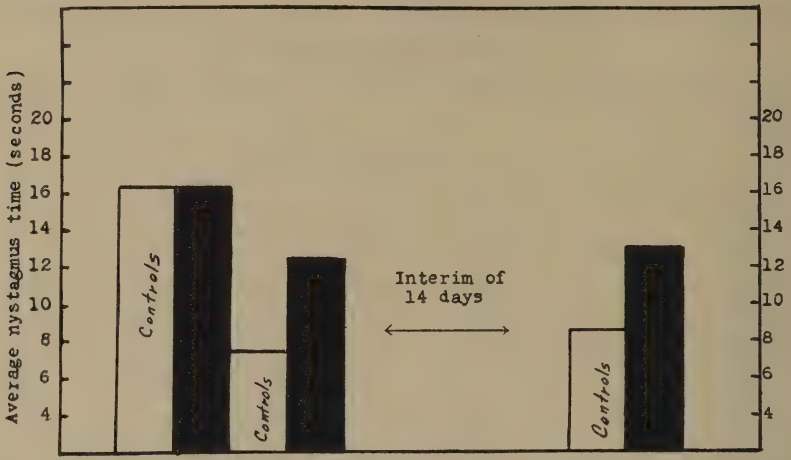

FIG. I. SHOWING HABITUATION EFFECT OF TEN DAYS OF SUCCESSIVE ROTATIONS ON DURATION OF POST-ROTATIONAL NYSTAGMUS IN CEREBELLAR (SOLID BLACK) AND NORMAL PIGEONS, AND ALSO DIFFERENTIAL RETENTION OF THE HABITUATION EFFECT

TABLE II

Showing critical ratios for group means in table I

	MEAN TEST I	MEAN TEST II	MEAN TEST III	MEAN HABITUATION	OPERATES			CONTROLS		
					Diff. I and II	Diff. II and III	Diff. I and III	Diff. I and II	Diff. II and III	Diff. I and III
Operates	16.5	12.4	13.2	21.6	16.5	12.4	16.5	16.7	7.6	16.7
Controls	16.7	7.6	8.7	54.6	12.4	13.2	13.2	7.6	8.7	8.7
Difference	.2	4.8	4.5	33.0	4.1	.8	3.3	9.1	1.1	8.0
σ Diff.	.200	.134	.181	.262	.118	.135	.161	.210	.181	.217
Diff./σ Diff.	1.00	35.8	24.8	126.0	34.7	5.9	20.2	43.3	6.07	36.8

The critical ratio for the means of Test I is 1.00. Expressed in terms of probability the chances are only 84 in 100 that the true difference between these two means is greater than zero. We prefer to follow the more conservative interpretation of such a ratio, viz., that the obtained difference is attributable to chance factors. For the means of Test II the critical ratio is 35.8. When a diff./σ diff. reaches the value of 3.0 the chances become 99.9 in 100 that the difference in question is a true difference. Thus a critical ratio of 35.8 represents practical certainty that further samples of the type considered here would exhibit differences in the direction of that obtained in the present instance. Similarly, the critical ratio of 24.8 for the means of Test III and that of 126.0 for the mean measures of habituation represent practical certainty of a true difference.

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[10] Such a ratio is commonly known as the critical ratio. Directions for computing this ratio are available in any standard text on statistical methods (cf. 31).

It is of interest to examine the relationships between the various measures or tests within each group. For the operated group the mean nystagmus time for Test I is 16.5 while for Test II it is 12.4. This difference of 4.1 is 34.7 times its standard error. This indicates that a significant change (habituation) had taken place within the period of time delimited by Tests I and II in the nystagmus behavior of the operated group. A similar fact is more strikingly revealed in the case of the control group, the difference of 9.1 being 43.3 times its standard error. Between the scores of Tests II and III the difference for the operates is 5.9 times its standard error; for the controls the corresponding critical ratio is 6.07. This suggests that both groups lost a significant amount of the habituation effect within a period of two weeks during which they received no rotational experience.

That considerable habituation effect is retained even after two weeks without reinforcement with rotational experience both for the operates and for the controls, is revealed by the differences between Tests I and III. For the operates the difference of 3.3 is 20.2 times its standard error; for the controls the difference of 8.0 (seconds) is 36.8 times its standard error.

SUMMARY

The findings up to the present point may be summarized as follows:†

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† November, 1935. As one part of the writer's research program as a National Research Fellow in the Biological Sciences, the major procedures reported in this monograph are being repeated. At this time substantial confirmation of the findings reported in statements (1), (2) and (3) above can be reported.

(1) There is probably no significant difference between the average duration of post-rotational nystagmus of birds with cerebellar lesions of the type considered here and that of control animals when tested for the first time under the conditions of this investigation.

(2) Successive elicitations of this response over a period of ten days results in a modification of it in the direction of extinction. This effect (referred to as "habituation") is exhibited in the records both of the operates and of the controls.

(3) With the same amount of rotational experience the habituation effect of (2) is significantly less in the case of birds with cerebellar lesions as compared with that of control animals, differences in favor of the latter being of the order of 2.5:1.

(4) When tested again after an interim of two weeks without additional rotational experience the two groups of animals in (3) both give records which reveal a significant loss of the habituation effect.

VARIABILITY

So far our comparisons of the operates and control groups have been based upon measures of central tendency. It is clear of course that the two groups also might differ as to either absolute variability or relative variability or both. Let us consider at this point the variability of the test scores noted in table I in terms of (1) mean deviation and (2) the coefficient of variability (mean deviation/mean). Table III presents these respective values.

None of the differences between the group average of the mean deviations or coefficients of variability is significant statistically. The critical ratios of these various differences at the bottom of table III provide the bases for these statements. It was also found that none of the differences between the various measures within either of the groups is statistically significant, these critical ratios ranging from .05 to 1.35.

Casual observations made at the time the data were secured had suggested to the writer that the operated group would prove to be somewhat more variable in its records for the various tests than the control group. That this expectation failed to be confirmed is indicated by the lack of significance of differences in table III. And further, the fact that the difference may fall in the opposite direction is strongly suggested by the following. The sigma of the mean as calculated for each of the group averages

TABLE III

Showing variability of measures in table I in terms of mean deviation and coefficient of variability

BIRD NUMBER	MEAN DEVIATION			COEFFICIENT OF VARIABILITY		
	Test I	Test II	Test III	Test I	Test II	Test III
	Operates					
G36	1.3	.3	.6	.130	.033	.054
G68*	7.4	2.2	6.3	.151	.086	.200
119	4.3	1.0	.6	.254	.107	.052
G52	2.1	.7	.9	.091	.047	.058
179	2.0	.4	.9	.115	.041	.081
213	2.1	.6	.9	.129	.042	.062
212	1.0	.9	1.1	.060	.078	.098
215	2.2	.7	.6	.176	.048	.037
223	1.9	.6	1.0	.093	.051	.083
G63	1.5	.8	.5	.099	.048	.032
Average.....	2.05	.67	.79	.126	.055	.062
	Controls					
G49	1.3	.4	.5	.125	.085	.068
G72	.2	.3	.7	.013	.040	.081
G38	1.8	.2	.6	.114	.050	.140
G57	1.3	.8	1.4	.065	.061	.099
G78	3.6	.5	.9	.190	.076	.104
286	1.4	.9	1.1	.085	.111	.124
279	.9	.7	.6	.114	.089	.070
283	1.4	.7	.8	.074	.078	.075
291	1.4	.8	.5	.074	.109	.074
298	1.0	.5	.5	.072	.064	.054
Average.....	1.43	.58	.76	.093	.076	.089
	Critical ratios for group means above					
Diff...........	.62	.09	.03	.033	.021	.027
σ Diff..........	1.34	.384	.380	1.090	.496	.616
Diff./σ Diff....	.46	.23	.08	.03	.04	.04

* Data for this bird not included in averages (see p. 99).

in table III was based upon ten scores (mean deviations). This procedure of course takes into account the variation in the record of each bird. It is interesting to note that individual variation within each group is sufficient to mask differences between groups. But for present purposes we are more concerned with possible differences in dispersion between a set of readings taken from a group of birds with a cerebellar lesion and a similar set secured from a control group. Table IV shows the standard deviation of each set of measures along with the Pearson Coefficient of Variation (V). For the operates each set of readings includes ninety observations; for the controls each set includes one hundred.

It will be noted that the σ's for the controls are consistently larger than those for the operates. This suggests that as a group the controls are more variable than are the operates. That they are relatively more variable also is revealed by the V's which also are consistently larger for the controls.

TABLE IV

Standard deviations and V's

	OPERATES			CONTROLS		
	I	II	III	I	II	III
σ	0.98	0.056	1.16	1.71	1.22	1.34
100 σ	98.00	5.60	116.00	171.00	122.00	134.00
Mean	16.5	12.4	13.2	16.7	7.6	8.7
V	5.94	.451	8.8	10.2	16.0	15.4

Concerning variability then we may say that while individual variation is sufficient to mask differences in group variation, when considered as a whole, the records (duration of nystagmus time) for the operated group are both absolutely and relatively speaking *less* variable than are the scores for the control group. This point will be considered somewhat in detail elsewhere (p. 75).

CORRELATIONS

Among the questions which come to mind as the data in the foregoing tables are examined some doubtless concern the degree of relationship between the different variables which are considered. For data such as the present degree of relationship between two variables is commonly expressed in some measure of correlation such as Rho (ρ). Rho is derived from the summated differences between the ranks of two corresponding sets of scores by means of the formula:

$$\rho = 1 - \frac{6 \Sigma D^2}{N(N^2 - 1)}$$

The value of ρ was calculated for each of the forty-five pairs of the following variables most of which are mentioned previously in tables:

1. Per cent lesion (i.e., of the entire cerebellum).
2. Mean score Test I (seconds duration of nystagmus).
3. Mean score Test II (for tenth day of successive rotations).
4. Mean score Test III (after two weeks rest period).
5. Habituation score (based upon difference Test I and Test II).
6. Retention score (ratio of scores of Test II to Test III).

The variables 7 to 10 concern the distribution of the lesion in four different regions of the cerebellum, based upon the amount of destruction appearing in each of four microscopic slides taken serially from the caudal portion forward for each brain. (See p. 80 for details of lesion analysis.)

7. Slide I (caudal-most portion cerebellum).
8. Slide II.
9. Slide III.
10. Slide IV (anterior portion of cerebellum).

Six additional ρ's were calculated which concern variability:

11. Mean deviation Test I.
12. Mean deviation Test II.
13. Mean deviation Test III.
14. Coefficient of variability Test I (MD/M).
15. Coefficient of variability Test II.
16. Coefficient of variability Test III.

The correlation table (table V) indicates the magnitude, probable error, and significance (based upon four times the P.E.) of some of the calculated ρ's.

TABLE V

Table of correlations

CORRELATION BETWEEN	P	P.E.	Signif.
Per cent lesion and mean score on Test I	−.13	.22	No
Per cent lesion and mean score on Test II	−.20	.21	No
Per cent lesion and mean score on Test III	.07	.22	No
Per cent lesion and *degree of habituation*	.09	.22	No
Per cent lesion and *measure of retention*	−.51	.17	No?
Per cent lesion and mean deviation Test I	.56	.16	No?
Per cent lesion and mean deviation Test II	−.05	.22	No
Per cent lesion and mean deviation Test III	−.12	.22	No
Per cent lesion and coefficient variability Test I	.59	.14	Yes
Per cent lesion and coefficient variability Test II	.18	.21	No
Per cent lesion and coefficient variability Test III	−.30	.22	No
Per cent lesion and lesion in slide I	.54	.16	No?
Per cent lesion and lesion in slide II	.62	.14	Yes
Per cent lesion and lesion in slide III	.94	.03	Yes
Per cent lesion and lesion in slide IV	.59	.14	Yes
Habituation and retention	−.40	.19	No
Habituation and mean score Test I	.79	.08	Yes
Habituation and mean score Test II	−.46	.18	No
Habituation and mean score Test III	−.45	.18	No
Habituation and lesion in slide I	−.20	.21	No
Habituation and lesion in slide II	.02	.22	No
Habituation and lesion in slide III	.37	.20	No
Habituation and lesion in slide IV	.60	.14	Yes
Retention and mean score Test I	.00	.22	No
Retention and mean score Test II	.68	.12	Yes
Retention and mean score Test III	.43	.18	No
Retention and lesion in slide I	−.13	.22	No
Retention and lesion in slide II	−.11	.22	No
Retention and lesion in slide III	−.75	.10	Yes
Retention and lesion in slide IV	−.73	.10	Yes
Mean score Test I and mean score Test II	.10	.22	No
Mean score Test I and mean score Test III	−.03	.22	No
Mean score Test II and mean score Test III	.90	.04	Yes

INTERPRETATION OF CORRELATIONS

While extended interpretation of correlations based upon as few cases as these is unwarranted, nevertheless certain possible relationships are indicated which furnish suggestions for further research. Whereas the correlation between per cent lesion and degree of habituation approaches zero, a negative relationship of $-.51$ (P.E. .17) is suggested between per cent lesion and retention. In other words, there is a tendency for birds with larger lesions to retain less of the habituation effect. Between habituation and retention a negative relationship of $-.40$ (P.E. .19) is also suggested.

It is of interest to note that while habituation and nystagmus time for Test I are correlated .79 (P.E. .08), the relationship between habituation and nystagmus time at the end of the habituation period is $-.46$ (P.E. .18). Thus the original nystagmus time of an operated bird (cerebellar) may be an index of the degree to which it will become habituated by a given period of rotations. On the other hand retention and nystagmus time on Test I are not related, while retention and nystagmus time on Test II are correlated .68 (P.E. .12). Thus the nystagmus time at the end of the habituation period may be an index of the degree to which habituation will be retained during a subsequent period of time.

The degree of relationship obtained between slides II and III and habituation and retention respectively suggests the desirability of more detailed analysis of the areas invaded by the lesion.

CHAPTER VI

THE EFFECT OF LESION UPON BIRDS PREVIOUSLY HABITUATED.

EXPERIMENT II

The material considered under Experiment I dealt with chronic cerebellar preparations, i.e., birds for which from four months to one year had elapsed between the operation in which they had acquired a cerebellar lesion and the beginning of the rotational tests described above. Such animals, we have seen, behave differently from normal animals in that with the same amount of rotational experience they become habituated to a significantly less degree. What effects can be noted when the cerebellar operation is performed *after* the birds have been habituated?

To secure data on this question two series (A) and (B) of twenty birds each were given a number of rotational tests somewhat modified from those previously described. These tests were briefly as follows:

Test I. Birds unselected; had had no previous rotation. Data and physical conditions similar to previous description (see p. 34).

Test II. Made on fourteenth day following Test I. Data and physical conditions similar to Test I. Birds had received ten periods of clockwise rotation per day on thirteen successive days prior to this test. While equivalent conditions were maintained throughout readings were not taken on twelve of these days.

Test III. Made two weeks after Test II. Data and physical conditions similar to Test I and II. Birds had received no further rotational experience following Test II and had lived under laboratory (cage) conditions until this test, with the exception to be noted.

Following Test II records of the birds were examined and a measure of habituation was computed for each bird. The birds were then divided into two groups equated as to the average amount of habituation to the successive rotations that had been acquired. The standardized operation was performed upon one of these groups of ten birds on the day following Test II. The other group served as controls. (For condition of birds following operation see p. 44.)

TABLE VI

Showing effect of cerebellar operation upon duration of after-nystagmus in a group of birds previously habituated to rotation

Critical test two weeks after operation

BIRD NUMBER	HABITUATION	MEAN TEST I	MEAN TEST II	MEAN TEST III	RETENTION	PER CENT LESION
			Operates			
267	49.4	24.5	12.4	20.5	60.5	58.4
262	49.0	22.2	11.3	26.5	42.6	40.0
263	61.3	15.2	5.9	8.3	70.0	21.0
242	67.0	14.2	4.7	8.7	54.0	43.6
247	71.0	14.1	4.1	9.8	41.8	65.4
252	67.0	20.6	6.8	17.5	38.8	66.4
259	45.6	21.9	11.9	18.5	64.4	35.6
265	58.0	16.9	7.1	11.1	64.0	48.7
246	70.0	18.0	5.4	7.6	71.0	36.9
268	49.4	14.2	7.2	10.2	70.5	21.3
Average . . .	58.8	18.2	7.7	13.9	55.3	43.7
			Controls			
250	63.0	16.8	6.2	5.7	108.0	
269	70.0	20.6	6.2	5.7	108.0	
258	45.7	20.8	11.3	13.1	86.4	
243*	66.6	19.7	6.6	Died		
248	73.0	17.0	4.6	5.2	88.5	
253	53.0	19.5	9.2	8.7	105.5	
254	62.6	19.2	7.2	6.8	105.6	
266*	33.0	15.2	10.2	Died		
255	53.0	17.9	8.4	6.8	123.0	
264	59.5	16.5	6.7	5.6	119.5	
Average . . .	59.9	18.5	7.5	7.2	105.0	

* Data for this bird not included in averages for group.

The experimental procedure for the series (B) was the same as the above except that Test III was given *four weeks* after Test II. The significance of the time intervals employed will be discussed elsewhere.

SERIES (A). CRITICAL TEST TWO WEEKS AFTER OPERATION

Table VI gives the means and related measures obtained for (A) whose critical test was given two weeks following the operation.

In this series, the two parts of the table falling to the left but including the data on Test II are directly comparable in that conditions were the same for both groups. Their records should afford therefore some indication of the reliability of the tests employed. It is true that the groups as presented here were previously equated upon the basis of degree of habituation (see p. 31). But the measure of habituation is in terms of *per cent* hence the equating process did not necessarily influence the magnitude of the group means for Tests I and II. The critical ratios of these particular differences (see table VII, p. 69) are too small to indicate true difference. It appears that we may safely infer a reasonably high degree of reliability associated with the tests in question. Further considerations bearing on this point will be discussed elsewhere (p. 77).

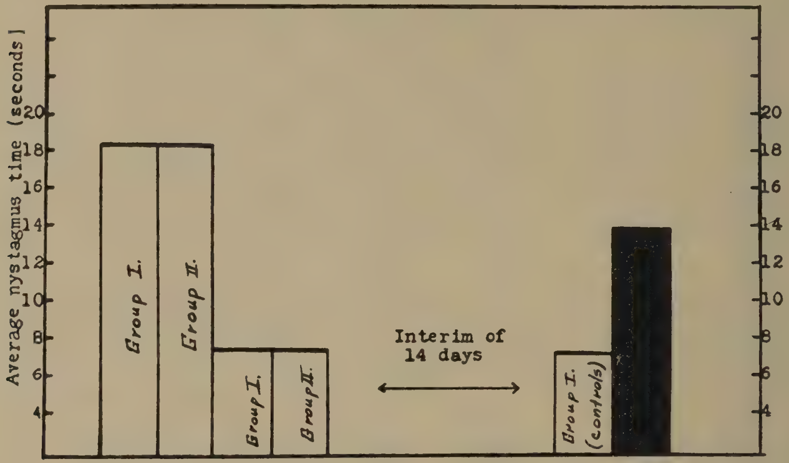


Fig. II. Showing Effect of Cerebellar Operation upon Duration of After-nystagmus in a Group of Birds Previously Habituated to Rotation

Examination of the critical ratios in table VII reveals evidence which concerns the effect of the lesion upon habituation previously acquired. This effect, it may be noted, is reflected in nystagmus time by a *loss or impairment of habituation.* The difference between the group means for Test III is 6.7, a difference that is 20.2 times its standard error. That the difference is primarily traceable to the operated group is indicated by the retention ratio of test scores II/III. Whereas the operated group retained approximately only fifty per cent of the habituation effect (based upon their mean score on Test II as a point of reference) the control group retained all or 100 per cent of the habituation effect.

TABLE VII

Critical Ratios

Series (A)

(Corresponding to means in Table VI)

	RETENTION	HABITUATION	MEAN TEST I	MEAN TEST II	MEAN TEST III	DIFF. II AND III OPERATE	CONTROL
Operates	55.3	58.8	18.2	7.7	13.9		
Controls	105.0	59.9	18.5	7.5	7.2		
Diff.	49.7	1.1	.3	.2	6.7	6.2	.3
σ diff.	.336	.924	.263	.198	.328	.594	.183
Diff./σ diff.	84.0	1.21	1.14	1.01	20.2	18.4	1.63

SUMMARY

The data for this part of the general study indicate that:

(1) When tested after a two-week interim without rotational experience two groups of habituated birds directly comparable (except that one group received cerebellar operation following habituation) showed marked difference in average duration of post-rotational nystagmus.

(2) The unoperated (control) group exhibited no loss of habituation effect while the cerebellar group showed marked loss of habituation to rotation.

(3) Placing a lesion of the type considered here in the cerebellum of birds previously habituated to rotation results in an impairment or reduction of the habituation effect as determined by subsequent tests.

VARIABILITY

A tendency was noted in the records of experiment (I) for the birds with cerebellar lesions to be somewhat *less* variable as a group in their response to successive rotations than a group of control animals. By examining the range of chance variation for different groups of unselected birds a necessary check upon the statistical significance of the above noted tendency is af-

TABLE VIII

Showing variability of measures in table VI in terms of mean deviation and coefficient of variability

BIRD NUMBER	MEAN DEVIATION			COEFFICIENT OF VARIABILITY		
	Test I	Test II	Test III	Test I	Test II	Test III
			Operates			
267	2.2	1.3	2.2	.090	.105	.107
262	1.9	1.1	2.7	.086	.097	.102
263	1.7	.7	1.4	.111	.118	.168
242	1.0	.4	2.7	.066	.068	.325
247	2.9	.4	1.5	.220	.098	.153
252	1.8	.5	2.7	.088	.074	.154
259	2.5	.4	.9	.115	.034	.049
265	1.3	.4	1.5	.077	.057	.135
246	1.0	.6	1.3	.056	.111	.171
268	1.6	.3	2.0	.113	.042	.196
Average ...	1.79	.61	1.89	.102	.080	.156
			Controls			
250	1.5	1.4	.4	.089	.226	.070
269	1.7	.6	.5	.083	.097	.088
258	2.0	1.2	1.0	.096	.106	.076
243*	1.1	1.0	Died			
248	.9	.7	.3	.053	.152	.058
253	2.3	.4	.6	.118	.044	.069
254	1.7	.4	.4	.089	.056	.059
266*	1.0	1.0	Died			
255	1.1	.9	.9	.062	.107	.132
264	1.0	.7	.5	.061	.104	.089
Average ...	1.52	.8	.57	.081	.111	.080

forded. This examination is made below. Table VIII gives the values for the mean deviation and coefficient of variability for series (A) based upon table VI.

Only one of the group differences is significant. The difference between the mean deviation on Test III is 1.32 and is 3.57 times its standard error. This indicates that birds in the operated group became more variable than their controls when tested after the operation. Examination of the σ's for the group scores considered as a whole also reveals greater variability on the part of the operates on Test III. Table IX (p. 71) gives these σ's with corresponding values of Pearson's Coefficient of Variation.

TABLE IX

Series (A)

Coefficients of variation

	OPERATES			CONTROLS		
	Test I	Test II	Test III	Test I	Test II	Test III
σ	2.21	1.54	3.00	1.29	1.12	1.34
100 σ	221.00	154.00	300.00	129.00	112.00	134.00
Mean	18.2	7.7	13.9	18.5	7.5	7.2
V	12.3	20.0	21.6	7.0	14.9	18.6

The significance of these observations is vitiated however by the fact that both the σ's and the V's of the operated group tended to be greater than those for the control group *prior to the operation.* A similar situation obtains in some of the data for series (B) to be considered below.

SERIES (B). CRITICAL TEST FOUR WEEKS AFTER OPERATION

In series (A) the critical test was made on the fifteenth day subsequent to Test II or on the fourteenth day following the operation. As was noted in a previous section (Observation Procedures, p. 52) this period is sufficient for marked recovery from the immediate effects of the operation manifested in overt behavior. It is also sufficient to secure a picture of de-myelinization associated with the lesion (see p. 82). While the theoretical point is a disputed one the possibility was considered that progressive degenerative processes set going by the lesion could act to augment post-rotational nystagmus. Birds with lesions tested within the time period occupied by such degenerative processes would thus show a *temporary* release from the habituation effects of previous rotational experience.

TABLE X

Showing effect of cerebellar operation upon duration of after-nystagmus in a group of birds previously habituated to rotation

Critical test four weeks after operation

BIRD NUMBER	HABITUATION	MEAN TEST I	MEAN TEST II	MEAN TEST III	RETENTION	PER CENT LESION
			Operates			
221	40.0	17.2	10.3	15.1	68.2	37.2
177	42.5	22.3	12.9	24.0	53.7	36.0
120	51.0	19.8	9.7	18.8	51.5	33.8
245	68.6	17.2	5.4	10.8	50.0	43.3
260	46.4	16.2	8.7	17.3	50.2	29.6
277	66.5	14.9	5.0	7.1	70.4	22.8
278	53.0	18.7	8.8	14.1	62.3	32.2
272	79.4	18.0	3.7	9.4	39.4	27.5
271	50.4	17.5	8.7	16.8	51.7	41.7
274	71.0	16.2	4.7	7.2	65.3	46.8
Average . . .	56.9	17.8	7.8	14.1	55.3	35.1
			Controls			
G79	47.0	22.2	11.8	10.9	108.0	
218	53.8	22.5	10.4	13.9	74.9	
257	51.5	16.3	7.9	9.9	79.8	
249	55.0	16.6	7.5	7.9	95.0	
220	66.2	24.0	8.1	11.1	73.0	
270	50.8	19.7	9.7	12.6	77.0	
261	69.0	15.1	4.7	7.7	61.0	
275	54.0	16.1	7.4	9.9	74.7	
276	75.5	22.0	5.4	7.7	70.2	
273	45.8	14.4	7.8	5.9	132.0	
Average . . .	56.9	18.9	8.1	9.8	82.6	

To investigate this possibility the experimental procedures of series (*A*) were repeated with a second group of twenty birds.

In this series *thirty* instead of fifteen days elapsed between the cerebellar operation and the critical test. It was assumed with some experimental basis (Weil, 83) that thirty days are sufficient for most of the degenerative processes to run their course. In line with the above mentioned possibility operated birds tested under such conditions might be expected to show no greater loss of habituation than a group of controls also kept for thirty days without rotational experience.

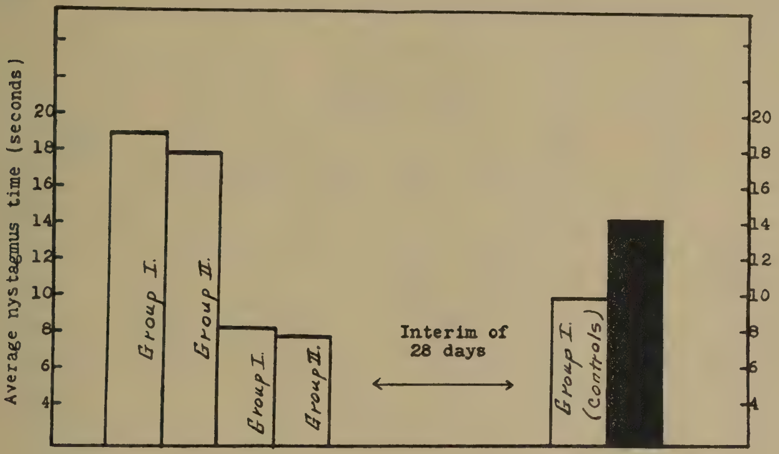


FIG. III. SHOWING EFFECT OF CEREBELLAR OPERATION UPON DURATION OF AFTER-NYSTAGMUS IN A GROUP OF BIRDS PREVIOUSLY HABITUATED TO ROTATION

That such expectation was not realized however is indicated by the data presented in table X. In fact the experimental results represent quite the contrary finding.

The difference of 27.3 between the retention scores for the two groups is 37.2 times its standard error. (See table XI.) Had the loss of habituation associated with the lesion been temporary in character the above difference should have approached zero. This would have demonstrated that the effect of the lesion upon habituation was temporary or ephemeral in character. But contrary evidence was obtained.

Some additional points in connection with table XI should be noted. While the difference of 27.3 for retention above is statistically significant it is also considerably less than the corresponding difference obtained in series (A). At least two factors may have contributed to this fact. One of them becomes apparent in the relationships indicated in table XII.

Under per cent lesion it may be noted that series (B) averaged approximately 8 per cent less lesion than did series (A). While every effort was made to standardize the operation (see Chapter III) it is possible that the operator unknowingly became more conservative in making the lesions in the birds of series (B).

TABLE XI

Series (B)

Critical Ratios

	RETENTION	HABITUATION	MEAN TEST I	MEAN TEST II	MEAN TEST III	DIFFERENCE II AND III	
						Operate	Control
Operates	55.3	56.9	17.8	7.8	14.1		
Controls	82.6	56.9	18.9	8.1	9.8		
Diff.	27.3	0.0	1.1	.3	4.3	6.3	1.7
σ diff.	.734		.254	.197	.289	.300	.181
Diff./σ diff.	37.2		4.33	1.52	14.8	21.0	9.40

TABLE XII

EXPERIMENT	PER CENT LESION	RETENTION DIFFERENCES IN FAVOR OF CONTROLS	CRITICAL RATIO
I	47.00	−6.4	7.1
II (A)	43.73	49.7	84.0
II (B)	35.09	27.3	37.2

Another possibility is that uncontrolled factors such as internal hemorrhage may have accounted for some of the difference in amount of destruction. Assuming for the moment a tendency for the correlation between size of lesion and retention to be negative (see p. 64) smaller lesions in series (B) would be accompanied by greater retention thus accounting in part for the smaller difference in the retention scores of the operated and control group actually obtained in this series. A second factor is that the control group also lost a significant amount of their habituation over the period of thirty days.

TABLE XIII

Showing variability of measures in table X in terms of mean deviation and coefficient of variability

BIRD NUMBER	MEAN DEVIATION			COEFFICIENT OF VARIABILITY		
	Test I	Test II	Test III	Test I	Test II	Test III
Operates						
221	2.2	.4	.5	.128	.388	.330
177	2.6	.4	2.4	.164	.310	.100
120	1.1	.6	1.1	.055	.062	.058
245	2.0	.7	.8	.160	.290	.074
260	2.1	.7	2.2	.129	.080	.127
277	2.6	.4	1.3	.174	.080	.183
278	1.4	.5	.6	.075	.057	.042
272	2.3	.6	.8	.127	.162	.085
271	.6	.4	.6	.034	.046	.036
274	.9	.3	.4	.055	.064	.056
Average...	1.78	.5	1.07	.110	.154	.109
Controls						
G79	1.5	.7	.6	.068	.059	.055
218	1.5	.5	.8	.067	.048	.058
257	1.4	.4	.4	.086	.051	.044
249	1.3	.3	.9	.078	.040	.114
220	3.3	.7	1.9	.137	.087	.171
270	1.3	.5	.5	.066	.052	.040
261	1.4	.6	.4	.093	.127	.057
275	1.6	.7	.5	.099	.095	.051
276	2.4	.4	.9	.109	.074	.117
273	1.4	.6	1.1	.097	.077	.187
Average...	1.71	.54	.80	.090	.071	.089

TABLE XIV

Series (B)

Coefficients of Variation

	OPERATES			CONTROLS		
	Test I	Test II	Test III	Test I	Test II	Test III
σ	1.59	1.48	2.61	1.99	1.30	1.26
100 σ	159.0	148.0	261.0	199.0	130.0	126.0
Mean	17.8	7.8	14.1	18.9	8.1	9.8
V	8.94	19.0	18.5	10.5	16.1	12.7

SUMMARY

The results for series (B) may be summarized briefly as follows:

(1) When tested after a four-week interim without rotational experience two groups of habituated birds directly comparable (except that one group received cerebellar operation directly after habituation) showed marked difference in average duration of post-rotational nystagmus.

(2) Both the control and the operated group showed marked loss of the habituation effect, however, the greater loss was noted in the case of the operated group.

(3) Placing a lesion of the type considered here in the cerebellum of birds previously habituated results in an impairment or reduction of habituation. This impairment of habituation may be noted when the critical test for duration of post-rotational nystagmus is made as long as four weeks after the cerebellar operation.

VARIABILITY

The data concerning variability for series (B) are little if any less ambiguous than those for series (A). The absence of any pronounced change in variability associated with the lesion is demonstrated in the group averages for table XIII. None of these differences is significant statistically.

A similar lack of significant change in variability is to be noted in the Coefficients of Variation in table XIV.

It is necessary to conclude that the effect of the cerebellar lesion upon variability of the response in question is *uncertain.*

CHAPTER VII

Control Experiments

EFFECT OF ANAESTHESIA

Besides having a cerebellar lesion the operated groups in series (A) and (B) differed from their controls in that they had been placed under the influence of a general anaesthetic (Nembutal) shortly after being habituated to rotation. The possibility was recognized that the subsequent marked loss of habituation by the operated birds might in some way be related to the effects of the anaesthesia rather than to the lesion itself.

To investigate this possibility five birds from the control group of series (A) were injected with the regular dosage of Nembutal (and thus placed in a state of general anaesthesia) on the day after Test III was made. Upon awakening, approximately two hours after induction of sleep, the birds were placed in their cages and kept without additional rotational experience for thirteen days. On the fourteenth day (after anaesthesia) the birds were given the standardized test for nystagmus. Their records for this test (IV below) along with those made on Tests II and III are given on table XV.

Chance differences and the time interval of two weeks without rotational experience are probably sufficient to account for the difference of 0.8 second between the averages for Tests III and IV. Thus no loss of habituation attributable to the influence of the anaesthetic is to be noted.

AUDITORY COMPONENT

The conditions under which nystagmus was elicited in the various experiments were complicated by the presence of an auditory component. This component was in the form of cessation of the hum of the motor driving the rotator and was always associated with the onset of retardation. This hum was estimated to be about that of G′ at 384 dv.

While the phrase "habituation to rotation" has been used freely in this report it cannot, strictly speaking, be regarded as legitimate usage. For it is clear that the property or properties of the stimulus situation to which the animal is said to become habituated are not known. There is some reason for believing that whatever these properties may be they are related to *ratios of excitation* (see p. 107). In a situation where normal animals respond (become habituated) let us say to a ratio of excitation between audition and deceleration-through-space a group of animals with defective hearing might conceivably (1) respond less (become habituated to less degree) to this particular ratio of excitation or (2) respond (become habituated) to some other ratio in the stimulus constellation.

TABLE XV

BIRD NO.	TEST II	TEST III	TEST IV
250	6.2	5.7	6.4
269	6.2	5.7	5.8
258	11.3	13.1	15.0
248	4.6	5.2	5.8
253	9.2	8.7	9.6
Average..........	7.5	7.7	8.5

TABLE XVI

OPERATES			CONTROLS		
Bird number	Test III	Test IV	Bird number	Test III	Test IV
G36	11.0	11.5	G49	7.4	8.0
119	11.5	11.0	G72	8.6	7.9
G52	15.4	16.5	G38	4.3	5.0
Average....	12.6	13.0		6.8	7.1

There was no reason to believe that the operation performed upon the animals used in this study directly impaired their auditory functions. However, no adequate checks other than for integrity of brain stem nuclei were made. It therefore seemed advisable to investigate the possibility of differential excitation with reference to the auditory component of the stimulus situation.

If habituation had been acquired with reference to some ratio of excitation directly involving audition either in the case of the operates or of the controls changing the character of the auditory component should result in a temporary (at least) loss of habituation. This hypothesis was put to a test in the following manner.

On the day following Test III (see p. 57) six birds (three operates and three controls) from the groups used in experiment I were again tested for nystagmus in the usual manner. This time however an electric buzzer (the alarm of an electric clock) of sufficient subjective intensity to mask all auditory cues associated with the rotator was kept going throughout the test.

That the change thus introduced experimentally failed to modify the state of habituation indicated by the records obtained on the previous day is shown in table XVI.

The obtained differences are sufficiently slight to be attributable to chance. The results thus indicate that the habituated (i.e., diminished) type of response to an objectively complex situation is not disturbed by a change in some of the auditory properties of the stimulus constellation. The theoretical significance of this particular control experiment will be discussed in a later section (see p. 107).

CHAPTER VIII

ANALYSIS OF THE LESIONS

A histological analysis performed on all of the operated birds was designed to yield information concerning (1) the extent or location of the lesion with particular reference to extra-cerebellar involvement and (2) a quantitative expression of the amount of cerebellar tissue destroyed in each case.

Only one instance of extra-cerebellar involvement was discovered. This bird (G68) was found to have suffered damage to underlying vestibular structures, particularly to the vestibular ganglia. The data for this animal are presented in a separate chapter.

In order to express the lesions in quantitative terms factors of shrinkage, distortion, connective tissue proliferation, heterogeneous character of the destroyed mass of tissue, and any irregularities in the shape of the lesions had to be taken into consideration. No correction was introduced for the shrinkage factor, it being assumed that with identical technique this factor would operate as a constant. Similarly, no effort was made to analyze the lesion into its various histological and neurological components. (Plans for further analysis in this direction have been formulated by the writer.) The remainder of the above mentioned factors were dealt with as described below.

TECHNIQUE

Each bird was killed by decapitation, the skull opened at three points to expose the brain, and the head placed at once into a 10 per cent solution of formalin. After fixing for 36 hours the brain stem with the cerebellum attached was removed and dehydrated by passing through 35, 70, 95 and butyl alcohol, the tissue remaining in each of these from one to two hours. From butyl alcohol the tissue was passed directly to 42 degree paraffin for one hour followed by 52 degree paraffin for another hour. Embedding was in the latter medium.

Each block was sectioned transversely and serially at 12 μ (with the exception of two blocks sectioned at 15 μ). Staggered mounting of a 20 per cent sampling of each ribbon of sections gave two sets of slides for each brain stem. One of these for each bird was stained for fibers by the Weil method; the other was stained with Cresyl violet, a cell stain. One brain stem (No. 119) was mounted serially in such manner as to yield four sets of corresponding slides. In addition to a Weil and a Cresyl violet series, a Davenport and a Van Guieson series was prepared for this bird. (For a summary of these four methods see Weil, 83).

Six brains showed little distortion as a result of the lesions. These together with a normal series made to control the technique and another normal series available in the laboratory were projected by means of a camera on coördinate paper. The area outlined by each section was determined directly in square millimeters. The eight brain stems were then grouped into two categories according to size. Five fell into the larger group; three into the smaller group. The average cross sectional area for each section was computed for each group. The two curves obtained by plotting these values represented the distribution through the dorsoventral plane of the cross sectional area of large and small brains respectively. A comparison of the two curves revealed a close similarity between the two. This fact was regarded as an indication that the sampling procedure had been reasonably accurate. The two curves were then taken as relative measures of the pre-operative shape (through a given plane) of the various brains.

An index of destruction was determined for each section by relating its lesion to cross rulings (of 25 square subdivisions) in the field of a binocular microscope. The summation of the cross sectional areas (taken from the above mentioned curves) of the various sections included by the respective index values for amount of destruction, multiplied by the thickness of each section gave a value for the volume of the lesion in each brain. This value when divided by that for the volume of the entire cerebellum yielded a percentage value for each lesion. It is this percentage value which is used for comparisons in this report.

RELIABILITY

To test the self-consistency of the observer in analyzing the lesions by the method just outlined, a sample of 100 sections was analyzed a second time, ten days after the first analysis had been made. The two values for destruction were compared for each of the 100 sections. When correlated this relationship was found to be .97 (P.E. .006), which indicates a high degree of consistency. The percentage values were found to agree within a range of plus or minus 5 per cent.

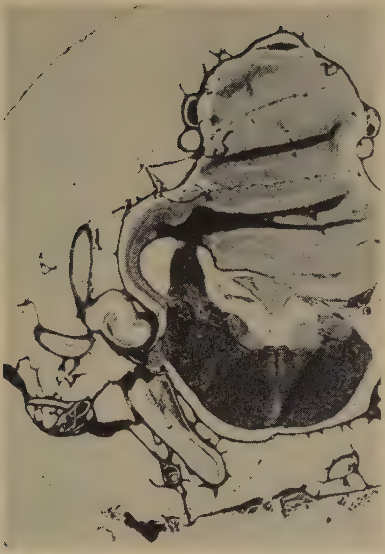
HISTOPATHOLOGY OF THE LESIONS

In terms of age the lesions were of three types. Type I consisted of lesions that were from four months to one year old; type II consisted of lesions that were four weeks old at autopsy. The histopathology of types I and II was found to be similar, indicating that the end-stage of degenerative changes was reached by the fourth week. It is possible to delimit the lesions in terms of three zones. Zone I was characterized by either the presence of necrose tissue or the complete absence of any tissue. Zone II consisted of a band approximately 1 mm. wide which surrounded zone I. In this zone both degenerated and healthy neural elements could be seen with a preponderance of the former. Zone III comprised another millimeter stripe outside of zone II. In this stripe the picture changed abruptly to a preponderance of healthy elements with only an occasional sign of degenerative change. In the two-week old lesions acute swelling of the nucleus and cytoplasm of the Purkinje and granular cells falling within zones II and III was observed; in the chronic lesions (types I and II) acute shrinkage of the cellular elements was observed in these areas. In instances of the latter the nuclei were either shrunken or elongated and darkly stained; the cytoplasms were homogeneously and darkly stained. Areas of hemorrhagic softening, anemic softening and glial proliferation were frequently observed in all three types of lesions. Every lesion exhibited marked demyelinization in the fiber layers.

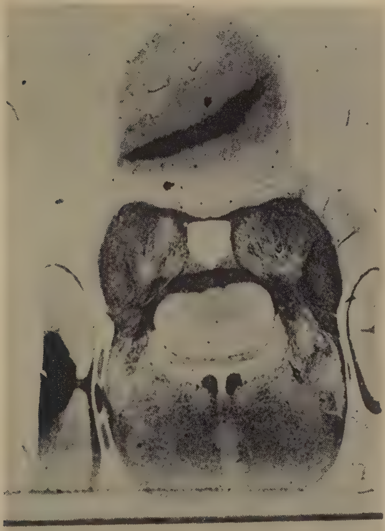
PLATES

PLATE I

I, SHOWING ANATOMICAL RELATIONSHIP BETWEEN CEREBELLUM AND VESTIBULAR STRUCTURES. *II*, SHOWING FIBER DISTRIBUTION IN REGION OF AURICLE. *I*, Davenport stain; *II*, Weil stain. 16×



I



II

PLATE I

PLATE II[1]

I. Section through vestibular ganglion of normal bird. Note density of cells. Davenport stain; 44×.

II. Same as I, through zone of entrance into brain stem of vestibular nerve. Note prominent axis cylinders. Davenport stain; 160×.

III. Section through left vestibular ganglion of G68. Note paucity of ganglion cells. Cells with pycnotic nuclei, homogeneously staining cells and empty capsules indicate degenerative changes here. (See p. 47.) Cresyl violet stain; 44×.

IV. Myelophage cells in cerebellar cortex surrounding lesion, with marked glial proliferation. Cresyl violet stain; 44×.

V. Section through anterior lobe of cerebellum showing virtually complete destruction of this region. Cresyl violet stain; 15×.

VI. Section through cerebellum of bird number 119. This bird was found to have approximately 85 per cent destruction. Weil stain; 10×.

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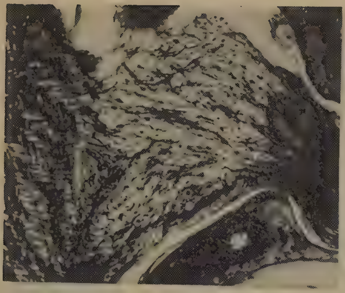
[1] The writer wishes to acknowledge the assistance of Dr. Glenn C. Dildine, of the Department of Zoology, Northwestern University, in the preparation of all photographic materials which appear in this dissertation.



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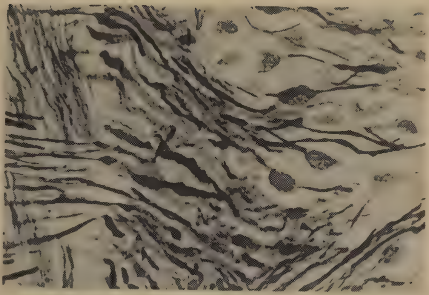
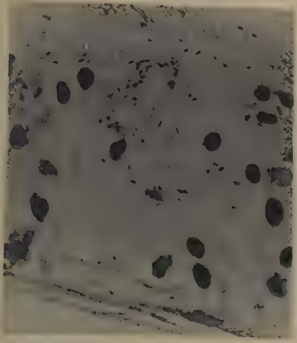
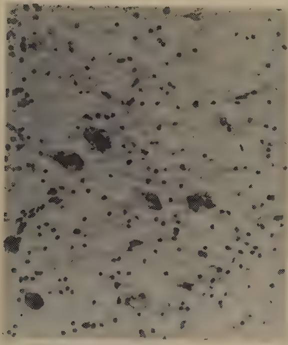


II



III



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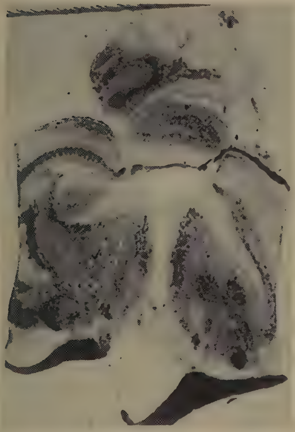
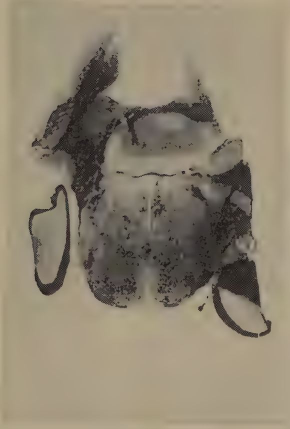


V



VI

PLATE II

CHAPTER IX

Re-establishing Habit Impaired by Lesion

A problem which the present study deals with only incidentally concerns the degree to which the loss of habituation associated with a cerebellar lesion is recoverable by further rotational experience. Evidence was presented in experiment I which may suggest that the lesion imposes a kind of rate "limit" upon the habituation process. Does the lesion also impose "limits" for modifiability of the response in question? No evidence is available as yet concerning this point. That there are certain qualitative differences to be noted in connection with the habituation process prior to the lesion and that subsequent to the lesion may be inferred from the following observations.

From the group of operated birds in series (A) of experiment II which had been given Test III two birds were selected in chance order for purposes of further study. This study took the form of analyzing their performances on the standardized test for nystagmus which was given to them on the five following successive days. Nystagmus time was recorded for each of the ten daily trials for each bird. Such data should yield information concerning the re-establishment of the habituated type of response.

The numbers of the birds employed along with their previous record of habituation et cetera are reproduced from table VI (p. 67).

BIRD NUMBER	HABITUATION	MEAN TEST I	MEAN TEST II	MEAN TEST III	RETENTION	PER CENT LESION
267	49.4	24.5	12.4	20.5	60.5	58.4
262	49.0	22.2	11.3	26.5	42.6	40.0

The post-lesion record of nystagmus time for each of the five successive test days is given for these two birds in table XVII.

There are several points of interest concerning the data in table XVII. The first to be noted is the marked disparity between the mean scores obtained in Test III and the magnitude of the scores obtained during the five successive days. Test III it will be recalled was made on the day immediately preceding that which marked the beginning of the five-day sequence.

TABLE XVII

TRIAL NUMBER	BIRD 267						BIRD 262					
	Duration of nystagmus											
	Day 1	Day 2	Day 3	Day 4	Day 5	Average	Day 1	Day 2	Day 3	Day 4	Day 5	Average
1	16.2	16.6	19.7	20.9	18.3	18.3	18.4	19.6	19.0	16.1	16.5	17.9
2	15.2	17.5	16.3	15.0	18.7	16.5	14.9	17.3	18.2	13.6	15.0	15.8
3	16.8	18.2	14.7	15.7	19.1	16.7	14.0	15.7	14.2	13.7	15.8	14.7
4	14.3	16.0	12.3	15.8	16.2	14.9	14.7	13.6	13.0	13.1	17.1	14.3
5	15.0	17.5	13.0	15.3	14.0	14.9	16.0	15.1	12.8	13.5	14.0	14.3
6	15.2	18.4	12.0	15.1	17.1	15.6	13.3	15.3	14.1	12.1	14.9	13.9
7	15.6	19.2	12.5	13.0	18.2	15.7	13.8	14.0	13.3	12.8	14.8	13.7
8	12.0	15.7	12.0	13.2	15.1	13.6	14.5	16.2	12.3	11.7	16.0	14.1
9	14.5	17.3	12.3	14.0	14.0	14.4	14.0	14.2	10.4	13.5	12.0	12.8
10	13.4	17.0	11.3	12.4	14.8	13.8	17.2	16.1	10.1	13.8	13.7	14.2
Average...	14.8	17.3	13.6	15.0	16.6	15.5	15.1	15.7	13.7	13.4	15.0	14.6

TABLE XVIII

TRIAL NUMBER	BIRD 267			BIRD 262		
	Test I	Test II	Test III	Test I	Test II	Test III
1	30.0	12.2	28.8	25.2	16.0	24.4
2	26.0	12.9	23.2	27.8	10.1	24.5
3	28.6	13.6	20.1	23.0	11.2	25.3
4	24.3	13.5	20.0	21.5	12.1	25.1
5	24.3	13.1	18.3	20.1	11.1	26.3
6	22.8	15.1	17.8	21.6	10.3	22.3
7	23.2	10.3	19.0	21.0	11.1	22.0
8	23.0	9.9	19.2	21.3	11.2	25.1
9	21.3	12.3	19.6	19.7	9.7	22.3
10	21.5	10.9	19.1	21.1	10.6	20.8
Average...	24.5	12.4	20.5	22.2	11.3	26.5

Examination of the individual records made by these two animals on their previous tests (table XVIII) yields little basis for understanding the marked (apparently spontaneous) drop in the nystagmus times observed in the records for the two days as noted above. The suggestion that we have here an example of the principle of "insight" or "closure" emphasized by Gestalt psychologists will be critically examined in a section dealing with general interpretations (see p. 114).

A point of particular interest in connection with the data in table XVII is the fact that the daily averages for the five days of rotational experience fail to reveal any positive evidence of habituation. This does not mean that these operated birds have been rendered incapable of re-habituation, however, for almost without exception the records for a given day exhibit evidence of considerable habituation effect. This fact can quickly be verified by glancing at the diminishing averages for the respective trials. Failure of the daily averages to reflect evidence of habituation indicates an *inability to retain* and thus to accumulate the daily increment of habituation effect contributed by each successive day of rotational experience.

Whether the level struck by the daily averages for the five days represents something in the nature of an "end-point" or "limit" for rehabituation or whether we have here an instance of *physiological plateau* frequently encountered in learning situations cannot be answered by the present data. Time did not permit an extension of this promising line of investigation beyond the five days, at the end of which time the animals were sacrificed for post mortem. It is proposed to explore these relationships further in another series of experiments.

CHAPTER X

Latency Changes Associated with Habituation

Casual observations made in connection with some preliminary experiments not reported here suggested to the writer the possibility that there might be some relationship between the latency of the quick component of post-rotational nystagmus and the amount of rotational experience which the animal had had. One theory, reviewed in an earlier part of this report, holds that the habituation process is essentially a "fatigue" phenomenon. In line with work done on other reflex latencies (30) if this theory were valid we might expect changes in the direction of increased latency of the quick component corresponding to the accumulation of the habituation or "fatigue" effect. A further reason for making an investigation of these relationships rested upon the possibility of differences in the performance of cerebellar and normal animals.

PROCEDURE

The following observations were made in conjunction with the first part of experiment I. By means of a procedure modified somewhat from that subsequently employed in experiment II both the latency of the quick component and the duration of post-rotational nystagmus were timed. To do this required the use of two split-second stop watches by the experimenter who went through a brief period of training to establish the manual coördination necessary for starting and stopping the watches.

A constant error of 0.20 seconds was introduced by starting the time for latency at the onset of retardation of the rotator. The latent period was regarded as ended (and nystagmus begun) at the first appearance of the quick component of nystagmus. Table XIX above shows the daily averages (uncorrected) for cerebellar and control birds along with the ten-day average for each bird. These relationships are represented graphically in figure IV below.

The timing method and the conditions under which the observations were made were in no sense ideal. These were probable sufficiently stable, however, to reveal any very gross change in the latent period in question associated with increasing habituation to rotation.

As may be seen in figure IV evidence of such a shift in latency is to be noted in the case of the controls between the first and the sixth days of rotational experience. For the operates this shift can be noted between the first and the seventh days. Following the high points of the two curves comes a rapid drop in both instances. The implications of this marked drop are by no means clear. With this point in mind it is of interest to examine the habituation records for the two groups over the ten-day period in which they received rotational experience. It may be observed from figure V above that the daily increment of habituation which varies considerably, when summated through the sixth day for the controls gives a value that nearly equals the total for the ten days. A similar but considerably less marked

TABLE XIX

Latency of quick component

DAY NUMBER	OPERATED BIRDS					CONTROL BIRDS					
	179	G52	119	G36	Average	G49	G78	G72	G38	G57	Average
1	1.4	3.6	1.2	1.1	1.8	1.2	1.4	2.7	1.1	2.0	1.7
2	1.2	2.5	1.1	1.7	1.6	1.0	1.2	1.4	1.1	2.7	1.5
3	1.2	3.4	1.1	1.3	1.8	1.3	1.7	1.2	1.5	3.6	1.9
4	1.9	1.9	1.1	1.5	1.6	1.3	1.4	1.5	1.9	3.3	1.9
5	1.3	1.8	1.2	1.2	1.4	1.8	1.4	1.5	1.9	2.9	1.9
6	1.2	2.3	1.1	1.6	1.6	1.8	2.9	2.0	1.7	4.1	2.5
7	1.3	5.2	1.3	1.0	2.2	1.6	2.1	1.6	1.8	5.1	2.4
8	1.3	2.3	1.4	1.2	1.6	1.1	1.5	1.4	1.9	3.5	1.9
9	1.3	3.3	1.1	1.5	1.8	1.7	1.2	1.1	2.0	3.2	1.8
10	1.2	2.0	1.0	.8	1.3	1.4	1.1	1.1	1.9	3.8	1.9
Average....	1.3	2.7	1.2	1.3	1.7	1.4	1.6	1.6	1.7	3.4	1.9

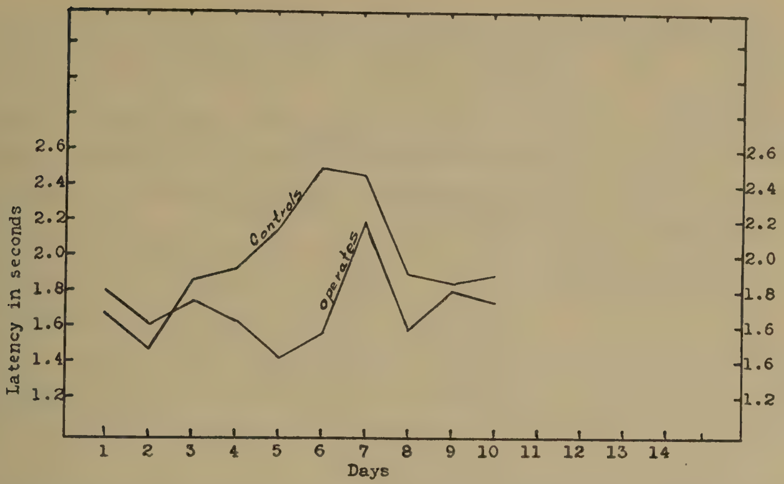


FIG. IV. SHOWING CHANGE IN LATENCY OF QUICK COMPONENT OF AFTER-NYSTAGMUS ASSOCIATED WITH SUCCESSIVE DAYS OF ELICITATION, IN OPERATED AND NORMAL BIRDS

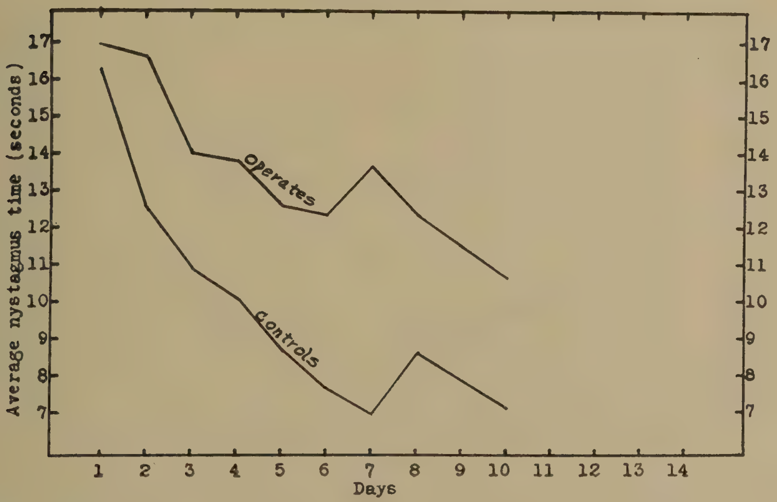


FIG. V. SHOWING DURATION OF AFTER-NYSTAGMUS ON SUCCESSIVE DAYS OF ELICITATION IN CEREBELLAR AND NORMAL PIGEONS

tendency is to be noted in the case of the operates. Discussion of certain suggestions growing out of these findings will be reserved for a later section (see p. 115).

The significant fact to be noted at this point in the general report is that no *consistent* change in the latency of the quick component of nystagmus associated with the habituation established by ten days of rotation apparently takes place. Some doubt is thus cast upon the validity of the theory which would account for all of the phenomena of habituation in terms of accumulated "fatigue" effects.

CHAPTER XI

RETENTION OF HABITUATION

Comparatively little is known concerning the permanency of the habituation effect in pigeons. An extended investigation of this problem by Fearing is now under way.

An opportunity was afforded in connection with the present general study to make tests for duration of nystagmus three months after the end of a ten-day habituation period. This interim of three months was not wholly devoid of rotational experience. On the fifteenth and seventeenth days respectively following habituation the animals were tested for nystagmus in the regular manner (except that on the seventeenth day rotation was in the counter-clockwise direction see p. 97) and were thus "practiced" somewhat. But since the effect of "practice" is probably always manifested in one direction under these condi-

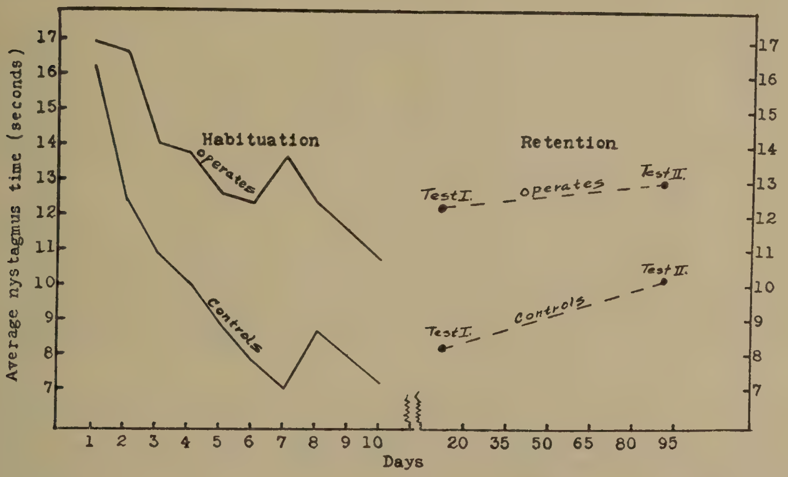


FIG. VI. SHOWING HABITUATION EFFECT AND RETENTION OF HABITUATION EFFECT IN CEREBELLAR AND IN NORMAL ANIMALS (PIGEONS)

tions (viz. towards increasing habituation) records secured after the three months' interim may be regarded as relative measures of retention.

The animals used were the same as were employed in the study of latency changes (see p. 57) and thus consisted of four cerebellar preparations and five controls. In figure VI below the habituation curves for the operated and control groups are reproduced from figure V. In addition points corresponding to average duration of post-rotational nystagmus on the above mentioned test days subsequent to the habituation period are plotted. It will be noted that both the operated and the control animals exhibit a marked habituation effect as long as three months after the end of the habituation period.

CHAPTER XII

TRANSFER OF HABITUATION

Conspicuous among the many controversial interpretations of the habituation process is that which concerns the degree to which habituation to rotation in one direction *transfers* to rotation in the opposite direction. Bárány (3) noted for human subjects (professional dancers) who whirl only in the clockwise direction a significantly shorter after-nystagmus for the "practiced" direction than that for the "unpracticed" or counterclockwise direction. Dodge (16) found that some habituation had taken place for the "unpracticed" direction but that considerably more habituation was obtained in the "practiced" direction. The ratio in favor of the latter was approximately 2:1. For pigeons Abels (1) and Mowrer (62) found nearly complete transfer of habituation. The latter stated (62, p. 33):

TABLE XX

Transfer of habituation

BIRD NUMBER	MEAN TEST I	MEAN TEST II	MEAN TEST III	MEAN (CC) TEST IV	PER CENT LESION
G36	10.0	9.0	11.0	6.6	55.0
119	16.9	9.3	11.5	11.1	83.6
G52	23.2	14.8	15.4	13.3	47.3
179	17.4	9.7	11.1	10.5	33.2
Average.....	16.9	10.7	12.3	10.4	54.8
G49	10.4	4.8	7.4	8.0	
G72	15.8	7.5	8.6	8.1	
G38	15.7	4.0	4.3	6.5	
G57	20.0	13.0	14.2	13.9	
G78	19.0	6.6	8.6	9.8	
Average.....	16.2	7.2	8.2	9.3	

> Repeated bodily rotation in only one direction, with vision excluded and with the successive periods of rotation and rest of equal duration, produces an equal reduction in the duration of the after-nystagmus elicited by bodily rotation in both the clockwise and in the counter-clockwise directions.

The present observations based upon a different stimulus situation from that employed by Mowrer also show marked evidence of transfer to the ''unpracticed'' direction. The birds with lesions exhibit complete transfer while the control birds exhibit somewhat less than complete transfer.

The animals tested for transfer effect were a part of a group of birds that were habituated to rotation by practice in the clockwise direction and tested for retention in connection with experiment I. The retention test (Test III) was made on the fifteenth day following the last of a ten-day habituation period. Two days later the birds were again tested in the usual manner except that rotation was in the counter-clockwise direction. The results of this transfer test (Test IV CC) along with the previous habituation record for each bird are presented in Table XX. A tentative interpretation of these findings will be reserved for a later section (p. 113).

CHAPTER XIII

Effect upon Habituation of Cerebellar Lesion with Damage to Underlying Vestibular Structures

So far the evidence concerning the relationships of the cerebellum to the habituation process has been taken from birds whose lesion was confined to the cerebellum. Here it is proposed to examine the records of a bird that in addition to a cerebellar lesion suffered damage to underlying vestibular structures. The histological analysis of bird G68 revealed marked evidence of degenerative changes in the region of Scarpa's ganglion, changes which were presumably attributable to the cerebellar operation. (See behavior data p. 45.) This bird was also given the various tests given birds in the first series of Experiment I including (and hereafter noted as)

Test I—Original test for nystagmus;
Test II—Test made at end of habituation period;
Test III—Made after interim of two weeks without rotational experience;
Test IV—Transfer test made two days after Test III;
Test V—Made three months after end of habituation period.

Table XXI gives the data for each test mentioned above. The various relationships are represented in figure VII.

From the data of table XXI graphically represented in figure VII it is evident that this neurologically ambiguous preparation differs from cerebellar and from normal animals chiefly in two respects. The first has to do with original duration of post-rotational nystagmus. G68, it will be noted, showed an original after-nystagmus time that was about 300 per cent that of either cerebellar or control animals. At the end of the habituation period the durations of after-nystagmus fell in the following order: longest duration G68; next longest cerebellar birds; shortest duration normal animals. The second point of difference con-

TABLE XXI

Nystagmus times for G68

TRIAL NUMBER	TEST I	TEST II	TEST III	TEST IV	TEST V
1	70.0	28.9	50.6	26.0	235.0
2	58.6	29.6	39.2	24.0	204.0
3	49.0	28.0	33.1	22.1	69.0
4	52.6	26.8	35.2	22.3	55.0
5	42.0	23.5	31.7	20.3	45.2
6	51.0	25.9	28.9	22.1	35.1
7	49.0	24.5	25.7	21.0	32.0
8	40.2	23.0	23.7	22.5	34.3
9	36.2	23.0	23.9	23.3	28.3
10	40.0	23.2	24.1	17.2	32.5
Average.....	48.9	25.6	31.6	22.1	65.9

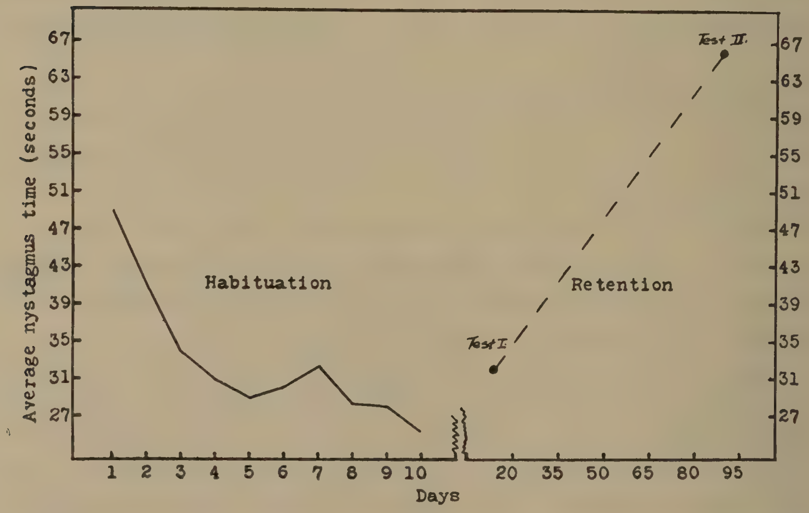


Fig. VII. Showing Habituation Effect and Retention of Habituation Effect in the Case of One Bird (G68) with Cerebellar Lesion and Damage to Underlying Vestibular Structures

(Compare with figure 6)

cerns the rate of loss of habituation effect. By the end of a three-month period G68 had lost more than 100 per cent of a previously established habituation effect whereas both cerebellar and normal animals had lost at a much slower rate. That such relationships as the above may serve to differentiate cerebellar and vestibular animals from either cerebellar or normal animals is a possibility which should prove of interest to the clinical neurologist.

CHAPTER XIV

Discussion and Interpretation of Results

RECAPITULATION OF PROCEDURES AND FINDINGS

Before proceeding to a discussion and interpretation of the various findings revealed in the present investigation, it is perhaps well to summarize briefly the various procedures and findings. Systematic observation of the behavior of birds with cerebellar lesions revealed the fact that marked "recovery" usually takes place within a two-week period following the operation. When after a period of from four months to one year following a cerebellar operation such birds were tested for duration of post-rotational nystagmus, nystagmus times characteristic of normal animals were found. In other words, the cerebellar lesion neither increased nor decreased the duration of after-nystagmus. In all animals, successive elicitation of after-nystagmus over a period either of ten or of fourteen days resulted in the usual modification of the response in the direction of extinction. Although both cerebellar and control animals exhibited this habituation effect, it was found to be much less marked in the case of the operated birds. When tested after a two-week interim without rotational experience two groups of habituated birds, directly comparable (except that one group had a cerebellar operation following habituation), showed marked difference in average duration of post-rotational nystagmus. Whereas the cerebellar group exhibited marked loss of habituation effect, the control group showed no loss. Similar findings were noted in a group comparable in all respects to the above with the exception that the nystagmus tests were made after an interim of four instead of two weeks. A significant degree of habituation was found to persist both in control and cerebellar animals for as long as three months after the end of the habituation period. Within this interval of time a significant loss of the effect had taken place in each instance, however.

PRELIMINARY STATEMENT OF PLAN TO BE FOLLOWED IN MAKING INTERPRETATIONS

In order to interpret the rôle played by the cerebellum in the above relationships it is necessary first to inquire into the nature of the habituation process. This inquiry will involve a brief examination of theories of learning. Since traditional discussions of the subject of learning have been restricted more or less to some particular type of learning, a generalized definition will be attempted. Similarly, traditional interpretations of cerebellar functions are not adequate for rendering the above relationships intelligible. Consequently in our discussion, various lines of evidence will be brought together upon the basis of which a theory of cerebellar function will be outlined.

In our survey of the pertinent literature we briefly examined four different theories that have variously been offered to account for the phenomena of habituation. These were (1) the peripheral theory, (2) the "fatigue" theory, (3) the central modification theory, and (4) the habituation as "learning" theory. Of these, the *learning theory* (and the *central modification theory* as a special instance) is the most satisfactory formulation for rendering intelligible the more rigorously controlled experimental findings including those of the present investigation. The considerations supporting this conception of the habituation process are discussed somewhat in detail below.

LEARNING THEORY OF HABITUATION

Many investigators have noted the similarites between "extinction phenomena," or more specifically the phenomena of habituation, and learning: for example Abels (1), Dodge (16), Griffith (34), Fearing (20), Razran (62), Robinson (71), and Lashley (56). Since for various reasons we are interested in testing this alleged similarity between the above mentioned processes it is necessary to examine the phenomena of learning. We may begin by adducing a general definition of learning.

Early attempts to describe the phenomena of learning dealt with learning as a process of *acquisition* of new modes of behaving (cf. discussion by Robinson, 71). According to this concept of learning, repetition (drill) acted as the "fixing agent" for the particular skill. In direct opposition to this point of view is one which conceives of learning by repetition in terms of *loss* of specific patterns of behavior (cf. Razran, 68). Comparatively few psychologists have conceived of learning explicitly in terms of a combination of these two processes of acquisition and loss. Dodge (16), whom we elsewhere cited as favoring a "learning" interpretation of the habituation process, apparently wavered between a combined and a single conception in terms of loss. He stated in 1923:

> Human learning always involves a negative factor. In some instances, the negative factor is dominant.
>
> . . . . Education is in fact very largely made up of the elimination of undesirable responses.

As noted in an earlier chapter the consideration of "extinction phenomena" as a development of the past two decades has demonstrated the need for drastic revision of learning theory.[11]

As a dual process (of acquisition and of loss in the sense of *organization*) learning is first of all conceived of as a process of ordering of *response potentialities*.[12] Learning is thus a selective process in that, of the many ways in which an organism may be capable of responding in a given situation, particular ways become "preferred." Thus a skill or a habit at first analysis exhibits an organization of behavior sequences or patterns. It is clear that the term *response potentialities* subsumes a stimulus situation. In other words, the organization or ordering of response potentialities must take place with reference to a particular situation. It is now a truism that an organism never responds twice in exactly the same manner. Variability is as much a fundamental characteristic of responses as response to stimulation is a fundamental characteristic of living protoplasm. Nor does learning alter this ubiquitous principle. The learned response is a variable response providing it be examined in terms of appropriately analytical units. Thus the "flawless" performance of the highly skilled singer may become an extremely "wobbly" performance to the discriminating "eye" of an oscillograph. While learning does seem to result in a reduction in the range of absolute variability of a response, it is not at all clear that any significant change in relative variability is associated with the "ordering" process. Lashley (53) found that relative variation in response for various stages in the acquisition of skill in archery approximated a constant. In our data the statistical constants which express relative variation tend to appear in groups or clusters.[13]

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[11] Cf. Dunlap's concept of "negative practice" (19b). Dunlap finds the traditional interpretation of the Law of Exercise (repetition) to be unsatisfactory. He points out that a skill is not acquired by practicing the response which is ultimately learned; one thing is learned by the doing of another:

"It is not to be assumed that the *learning responses* are responses of the same kind as those which are *learned*. The billiard shots through which one learns to play billiards are, in one sense, of the same type as those he makes after he has become proficient. They are muscular movements which propel the cue longitudinally against the ball. But considered and measured more carefully, the early shots turn out to be different from the later in very important respects. By one type of response, apparently, the reactor learns to make a quite different type of response" (p. 14).

Although formulated chiefly as a clinical hypothesis, Dunlap's principle finds some support in recent experimental work by Kellog *et als*. Curiously enough, Dunlap has almost completely ignored the phenomena of experimental extinction in his discussion of learning, in spite of the fact that it was he whose observations precipitated the wartime controversy concerning the validity of the Bárány tests in selecting army aviators (see discussion by Mowrer, 62).

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[12] The term *response potentialities* may require clarification. A "prelearned" state is arbitrarily assumed in which an organism is capable of making many specific reactions with reference to a stimulus situation. These specific reactions or *response potentialities* lack functional organization, however. When presented with a stimulus situation such an organism may tend to "dash off in all directions at once": in other words, respond in an unpredictable manner. By learning, this tendency towards random response is altered.

[13] The writer has observed a similar effect in connection with certain observations on the righting response in planaria. Adults and pieces of planarian tissue were studied. Clustering of the statistical constants for relative variability was found to persist in the presence of marked regional differences in absolute variability of the response in question; it may possibly reflect the dominant organization system common to a part or to an adult organism. The range of absolute variability would thus reflect the influence of competing but always less dominant

We have indicated that learning represents directional organization of response potentialities. It is necessary to consider the nature of this organization. Watsonian psychologists have mostly ignored the factor of variability in interpreting the phenomena of learning. As a result they conceived of the organization characteristics of a trained animal more or less as a kind of "machine gun" type of organization. An unlimited supply of identical responses (bullets) were made available by conditioning for firing towards any object or situation setting off the appropriate mechanism (trigger). If it were possible to think of the many response potentialities of an organism at any stage of learning in terms of the load of a shot gun, the individual shot of which were quite irregular in shape resulting in variable patterning of the load upon discharge, an analogy somewhat more in keeping with the facts of behavior would be afforded.

The total pattern of organization characteristic of learning is closely related to varying degrees of predictability. The maze behavior of a rat undergoes successive changes (i.e., a process of ordering) in the direction of *increased probability* that the goal will be reached as learning of the habit proceeds. Predictability implies recurrence in time which in turn subsumes the fact that the ordering process of learning has taken place with reference to or along a time axis. To come under the heading of a skill or a habit the duration of the behavior sequences must fall within certain critical limits of time.

Before setting up our definition of learning there are yet other considerations. We have so far referred to *a stimulus situation* with reference to which ordering of responses takes place. The investigations of Lashley (54a) and Klüver (51a) have shown that as far as the behavioral significance of *a stimulus situation*

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systems. It is of interest to compare in this connection Coghill's (11a) description of the development of behavior patterns in Amblystoma and Child's discussion of the development of the nervous system (11). The above observations grew out of a problem suggested to the writer by Professor James W. Buchanan of the department of Zoology, Northwestern University and were made on a species of Euplanaria supplied to the writer by him.

is concerned its "objective" properties are extremely ephemeral in character. Lashley (55) concluded:

> . . . . within very wide limits, the absolute properties of the stimulus are relatively unimportant for behavior and the reactions are determined by ratios of excitation which are equally effective when applied to any group of receptor cells within the system (Lashley 1924b).

Klüver has emphasized the *phenomenal* properties of the stimulus situation:

> Whether or not behavior takes this or that direction is, generally speaking, dependent on whether or not this or that *phenomenal* property exists. The fact that something appears phenomenally as "red," "larger than," etc., cannot be deduced from a study of radiation or from the properties of the atom but only from studies of reacting organisms (51a, p. 332).

and elsewhere:

> The fact that in many instances we are not able to say what the determining phenomenal ratios or properties are does not mean that we can ever hope to gain insight into behavior by relating physiological, neurological, biochemical, etc., data directly to objective ratios or properties. So far as behavior is concerned, it can be experimentally demonstrated that the *objective* ratios are not the final word. The ratios which count are not spatial ratios, ratios of intensity, etc., at least not if these terms are objectively used; the ratios which count are phenomenal ratios (*ibid.*, p. 342).

With Lashley, he has also stressed the importance of *equivalence* of two or more stimulus situations: the fact that organisms may tend to respond in the "same" way to situations which are objectively quite dissimilar.

Taking into account all of the foregoing necessary qualifications we may now attempt a generalized definition of learning. Learning may be defined as an ordering along a time axis of response potentialities with reference to a stimulus situation or its equivalent.

TYPES OF LEARNING

Psychologists generally recognize four types of learning. These are usually termed "rote learning," "maze learning," "insight learning," and "conditioned-reflex learning" respectively. Rote learning commonly refers to such acts as memorizing of material such as poems or nonsense syllables. The familiar Laws of Association (contiguity, frequency, vividness, etc.) were originally formulated with reference to this type of learning. Maze learning is a type of learning which has been studied chiefly by animal psychologists. The problem is presented to an animal in the form of a maze to be run in reaching some goal such as food. Like rote learning, maze learning generally exhibits improvement by repetition. Traditionally this improvement has been regarded more or less as a *continuous function* of repetition. In recent years this interpretation has been called into question. Lashley for example has stated:

> It is not our purpose to minimize the importance of exercise for learning, but only to point out that the facts of improvement with practice are susceptible of various interpretations and do not justify the usual inferences drawn from them concerning the nature of the nervous processes involved. Associative connections are strengthened by practice but it does not follow that these connections are nerve tracts in which resistance is lowered by repeated passage of impulses. On the contrary, the changes in the character of the responses with practice indicate the continuous formation of new associative bonds, and there seems to be no instance of learning on record to which this explanation of the law of exercise could not apply (56, p. 484).

Insight learning is a type of learning which has been emphasized by the Gestalt school. According to the latter, organismic activity is goal-directed activity. In the early stages of learning (the pre-goal stage) the goal-seeking activity is incomplete or "unclosed." Under appropriate conditions spontaneous "closure" or reaching of the goal occurs. This spontaneous "closure" is frequently referred to as "insight learning." Klüver has found that a single instance of spontaneous "closure" (correct solution) may so fix the solution of a particular problem for a monkey that this solution may be spontaneously "recalled" as long as three years later. Lashley finds the insight or "closure" principle inadequate as an operational concept of learning. He states:

> As applied to learning, there is no present criterion of closure of a system of activity except the fact of learning so that, if the hypothesis does not beg the question, it at least is inapplicable in advance to any particular learning problem (56, p. 486).

Conditioned-reflex learning has been exploited as "the principle of all learning" in the physiological laboratories of Pavlov and Bechterev. Hull is the chief proponent of this type of learning among psychologists. He has recently summarized the experimental data for this type of learning (64a). Two different types of reactions have been uncovered by conditioning experiments. One of these Hull terms an Alpha type "which are merely sensitizations or augmentations of the original unconditioned reaction of the conditioned stimulus; these will have relatively short reflex latencies." The second or Beta type "results from the acquisition by the conditioned stimulus of the power of evoking reactions at least functionally similar to that evoked by the unconditioned stimulus; this type will have a latency substantially that of ordinary voluntary reactions."

Hilgard and Marquis, 1935 (40) have emphasized the novel character of the conditioned reaction:

> It is highly significant that the conditioned response develops slowly and progressively. If the conditioned response is considered as a fully integrated reflex which is shunted from the unconditioned stimulus to the conditioned stimulus it is natural to expect that it would be full strength on its first appearance. . . . The conditioned reflex can better be regarded as a *new* response which develops in the particular situation . . . The novelty of the conditioned response as it develops in an experiment consists not in any single descriptive characteristic, but rather in a set of functional relationships. Among the criteria of conditioning found useful in our analysis were the progressive alterations in frequency, amplitude, and latency of the responses with practice or during extinction.

RELATIONSHIP OF THIS DEFINITION TO VARIOUS TYPES OF LEARNING

To evaluate critically here the details of the relationship of our definition of learning to each of the foregoing types would take us far afield. It must suffice only to indicate that there appears to be no phenomena peculiar to any known type of learning which would invalidate our definition. On the other hand it can be shown that the definition does differentiate the phenomena of learning from certain other types of phenomena.

PHYSIOLOGICAL BASIS OF LEARNING

In spite of assumptions to the contrary the neurologist and physiologist have contributed extremely little to an understanding of the *modus operandi* of learning, regardless of type. To be sure, ingenious models have been constructed, elaborate diagrams designed, analogies with such phenomena as hysteresis of linseed oil, the behavior of polyphase colloidal systems, neurone growth, "fatigue," and "going stale" have been pointed out. But it must be concluded that whatever the physiological mechanisms underlying learning are, they are as yet unknown. Certain broad principles of growth or development as indicated by the searching studies of Child, Coghill, and Herrick do afford suggestive leads.

Child (10) has emphasized the rôle of physiological gradients in regulating developmental pattern. These gradients seem to have their origin in polarity of physical, chemical, and electrical interrelationships between the various parts of a growing organism. Coghill (11a) has stressed the principle of functional unity in the elaboration of primitive behavior patterns. By a process of progressive individuation from a total or organismic pattern, the growing animal achieves greater and greater specificity in its reactions. But always the total pattern of reaction is the dominant pattern. It is highly significant that individual reactions are never "plugged in" on the total pattern but only functionally related groups of reactions. This fact is in line with Herrick's careful analysis of the neural relationships in the brain of Necturus. Here in a primitive brain anatomical evidence of isolated reflex or reaction units should be most conspicuous. But on the contrary, Herrick has found a most amazing degree of anatomical complexity associated with, relatively speaking, simple reflexes (cf. 37c).

The individual and collective contributions of these three men, to our understanding of the processes of organic development, combine to firmly establish the broad principle of development as a dynamic ordering of response potentialities with reference to a total or unitary pattern. Evidence is accumulating from many sources which indicates that this principle holds whether we be concerned with the history of muscle, gland, brain or adult. While it is clear that the *modus operandi* of either is unknown, we may recognize that growth and individuation as principles of biological development closely parallel those of growth and regression (as in learning by concomitant processes of acquisition and loss) as principles of psychological development. It appears likely that the same order of analysis will be required for an understanding of both.

THE RELATIONSHIP OF HABITUATION TO LEARNING

We have defined learning generally as an ordering along a time axis of response potentialities with reference to a stimulus situation or its equivalent. Do the phenomena of habituation come under this definition? Although we have not explicitly indicated all of the various phenomena included under the four types of learning which were briefly examined, some of these are noted incidentally below. By comparing the phenomena of habituation with phenomena termed "learning" it is believed that a fundamental similarity between the two processes is revealed. In this connection we may examine the following lines of evidence as found either in the present study or in the literature bearing on habituation: (1) acquisition of response to rotation, (2) properties of habituation curve, (3) variability changes associated with habituation, (4) retention, (5) re-establishment of habituation, (6) transfer of habituation, (7) spontaneous improvement, (8) latency changes associated with habituation, (9) central character of habituation.

(1) *Acquisition of response to rotation*

From the preliminary studies of Stoltenberg and Fearing (80) and Fish and Windle (27) evidence was reviewed which indicates that response to rotation is but little (if at all) developed at birth; it undergoes rapid development during the three to five weeks subsequent to birth at the end of which time responses characteristic of the adult are found. Stone (80) regards this sequence as evidence of a process of maturation related synchronously with a stage of development at which the response becomes useful. It is possible to criticize this interpretation on the grounds that the term "maturation," when related to behavior is extremely vague and even misleading. Attempts to relate myelinization to "maturation" of behavior patterns have been unsuccessful (cf. Hooker's work on human fetuses). However, it is probably significant that the response with which we are dealing, and which under appropriate conditions tends to disappear with successive elicitations, does not reach its maximal development until several weeks after birth.

(2) *Properties of habituation curve*

It is of interest to note that the habituation curves obtained here and in other studies are characterized by an early period of positive deceleration followed by a period of negative deceleration. Thurstone and other psychologists regard such a curve as representative of learning curves. Curves of similar design are usually obtained in the extinction phase of conditioned reflexes (cf. 40).

(3) *Variability changes associated with habituation*

The data of the present investigation indicate that there is a reduction in absolute variability associated with the habituation process. Thus the variability in duration of response at the end of an habituation period is much less (in absolute terms) than at the beginning of habituation. On the other hand, it is not clear that any significant change occurs in relative variability of the response in question. These observations are in line with those made by Lashley (53) on development of skill in archery.

(4) *Retention*

While we have not discussed "retention" explicitly in connection with learning it is clear that this factor is implicit in our definition. The laboratory test of whether something has been learned becomes a test ultimately of whether it has been retained. Many writers hold that the learned act is characterized by gradual loss or decrement with time. It is probably significant that habituation exhibits this phenomenon of gradual loss when not re-inforced by practice. After a period from three to four weeks following the end of the habituation period, all animals examined in this connection in the present study exhibited the beginning of a gradual diminution of habituation effect. Our data also indicate that both cerebellar and normal animals may be expected to exhibit a marked habituation effect as long as three months after the end of the habituation period. A similar observation in connection with conditioned eyelid reactions has been reported by Hilgard and Marquis, 1935 (40): "conditioned eyelid reactions may be retained for periods as long as three months." Examples of even longer periods of retention are commonplace for rote learning and by no means rare for insight and maze learning.

(5) *Re-establishment of habituation*

Our attempt to re-establish the pre-operative level of habituation in the case of two birds failed for a five-day period of successive elicitations. However, Griffith (35) found that "the time taken to reduce post-rotational nystagmus in a second series (i.e., second period of habituation) is notably shorter than the time taken in the original practice series." This observation is also in line with those of Hilgard and Marquis (see above): "Relearning after long periods was shown to require but one-tenth of the trials to reach a given amplitude as were required for original learning." Again similar findings in the case of rote learning and maze learning are commonplace.

(6) *Transfer of habituation*

Certain of our data, which are in agreement with those of Mowrer (62) and others, indicate that habituation by rotation in one direction transfers almost completely (both for cerebellar and normal animals) to the "unpracticed" direction. Learning experiments concerning transfer of training have yielded conflicting results (cf. Lashley, 56). However, more carefully controlled studies on conditioning have revealed that conditioning is specific for a given range of stimulus conditions but within such a range conditioning is generalized. A similar interpretation is possible for the phenomena of habituation. Maxwell, Burke, and Reston (59) found habituation to be specific for certain conditions of elicitation: "It should be mentioned that when the after-nystagmus following rotation at the rate used in these experiments had wholely ceased to appear, a vigorous after-nystagmus could be obtained by using a more rapid rate, say 10 turns in 10 seconds." Holsopple (43) holds that the extent to which habituation is generalized (i.e., may involve both the practiced and unpracticed directions) depends upon the temporal intervals at which successive elicitations occur.

(7) *Spontaneous improvement*

Proponents of insight learning have stressed the significance of spontaneous or sudden improvement (as opposed to gradual improvement by trial and error) as a criterion of learning. Examples of spontaneous improvement of conditioned reflexes may be found in the literature (cf. 40). Our observations with two birds for which we attempted to re-establish the pre-operative level of habituation should be noted in this connection. On the day on which these birds were given a critical test (Test III, see p. 88) for duration of post-rotational nystagmus their average nystagmus times were 20.5 and 26.5 seconds. The longest reading secured for each on the next day (i.e., the beginning of their training period) was 16.8 and 18.4 seconds respectively. This instance of spontaneous improvement in habituation was a wholly unexpected finding. It is tempting to invoke the Gestalt principle of "closure" in this connection, but until such relationships as suggested by these limited observations can be explored further interpretations are of dubious value.

(*8*) *Latency changes associated with habituation*

Hull (64a) and Hilgard and Marquis (40) have pointed out the significance of latency changes associated with the establishment and extinction of conditioned reflexes. While the method by which we made some observations on latency changes associated with habituation is open to serious criticism, it did reveal suggestive evidence that the early period in the habituation process (i.e., the first four to six days) is characterized by progressive increase in the latency of the quick component of after-nystagmus.

(*9*) *Central character of habituation*

We have reviewed various types of indirect evidence derived from studies by Dunlap (18), Gould (32), Fearing and Mowrer (26), Schmaltz (78), Lorente de Nó (57) and others, which indicates that the habituation process takes place within the central nervous system. The present study has revealed direct evidence of this fact. Birds with cerebellar lesions have been shown to become habituated to a significantly less degree than normal animals when given the same period and number of successive rotations. Similarly, the effect of a cerebellar lesion upon birds habituated to rotation has been shown to be an impairment of a significant part of the habituation effect. In other words, it has been shown that habituation takes place within the central nervous system and further, that the cerebellum participates directly in this process. The demonstration that habituation is central in character is in line with similar demonstrations of the central character of maze learning (cf. Lashley 55), and opposes the interpretation made by King (51) as a result of his failure to find evidence of disturbance of habituation associated with decerebration. The demonstration that the cerebellum participates directly in the habituation process is in line with no other studies of cerebellar functions as reported in the literature and requires detailed examination.

It will have been noted that in showing the relationship of habituation to our definition of learning, we found it convenient to relate the phenomena of habituation directly to phenomena observed in the various types of learning included under our definition. Various methods might have been adopted, but our aim has been to compare phenomena as revealed by experiment and to avoid discussion of purely dialectic significance. No one of the foregoing factors associated with habituation may be said to establish it as a "learning" phenomenon. However, all of them in combination appear to justify the conclusion that habituation of post-rotational nystagmus by means of repeated elicitation is a process of the nature of learning.

THE CEREBELLUM AND MAZE LEARNING

As far as we have been able to determine, only one experimental study has been reported in which the relationship of the cerebellum to such processes as learning has been explored. Lashley and McCarthy, 1926 (54) trained seven rats to 10 errorless trials on a rectangular maze with eight culs de sac. After 10 days without practice, retention was tested by retraining until the criterion of 10 errorless trials was again satisfied. Extensive cerebellar lesions were then made in all of the animals, two of which were also blinded by enucleation of eyeballs. Following a 10-day recovery period ("for most") the animals were again tested on the maze. Lashley and McCarthy concluded:

> In both seeing and blind animals perfect retention of the habit was demonstrated after the operations. One animal with the cerebellum completely destroyed learned to run the maze without error. *There is no evidence that the cerebellum plays any part in the performance of the maze habit.*[14]

In order to examine critically the basis for the above conclusion we have reproduced a part of the published data for this study. (Table XXII.)

It will be noted that in every instance the time factor has been markedly increased by the cerebellar lesion. Thus the statement quoted above that there is no evidence that the cerebellum plays any part in the performance of the maze habit is clearly not justified by their own data. Such a conclusion could follow only if we were to accept as the criterion of the maze habit the extremely gross one of successfully getting through the maze. It seems obvious that such a criterion might obscure differences relatively as great as, for example, differences in performance on the hundred yard dash of a trained sprinter and an aged man. Both could doubtless traverse the distance but one might conceivably *require* 10 times the number of seconds of the other in getting there. Just as factors of "age," lack of training, etc., would operate to impose a differential "rate limit" upon the performance of the runners in our example, a cerebellar lesion would appear to impose a kind of "rate limit" upon the performance of a white rat in a maze situation. Since in many types of situations "rate" of performance is the critical factor in determining "successfulness" of an act, we may profitably examine some of the implications of this suggested phase of cerebellar functions. But first we should indicate some of the questions which Lashley and McCarthy did not and have not since answered: (1) Were changes in "motivation" introduced for the operated animals? (2) Was there any histological evidence of extra-cerebellar involvement, particularly of vestibular structures? (3) Were the animals retrained after the operation able to *retain*? (4) Is a ten-day period sufficient time for the permanent effects of a lesion to be manifested? (5) How would chronic cerebellar preparations perform on such a maze problem?

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[14] Italics mine.

TABLE XXII*

ANIMAL NUMBER	PRELIMINARY RETENTION TESTS			POST-OPERATIVE RETENTION TESTS		
	Time	Errors	Trials	Time	Errors	Trials
	seconds			*seconds*		
2	169	4	11	657	14	19
3	434	7	19	1,403	9	15
4	229	7	11	801	0	10
5	2,464	52	48	5,337	97	78
6	107†	1†	11†	188	0	10
7	129†	0†	0†	182	0	10

* Table 1, from Lashley and McCarthy (54).
† After enucleation of eyeballs.

When it is appreciated that modern theories of cortical mechanisms rest, in some instances, indirectly upon the allegedly negative and, in any event, extremely limited data of the above experiment, the need for careful examination of the possible rôle played by the cerebellum in the so-called "higher processes" becomes apparent. In developing a theory of cerebellar function in the following, it is suggested that theories based upon the idea of autonomous cortical mechanisms are in error and that "cerebration" as the term is frequently used, is without justification. Cerebration, we believe, is always a process of *cerebration* and *cerebellation*.

SYMPTOMS AS "DISPERSION" OF RESPONSE POTENTIALITIES

In our discussion of the symptoms which appear (then disappear) after cerebellar lesions we noted three general periods of post-operative behavior; a period of shock (great disturbance), a period of re-constitution (reappearance of normal patterns), and a period of redintegration (during which a structurally altered organism may behave as a normal animal). It seems probable that what we observe during the period of shock represents a reversion to a more primitive or "less-individuated" level of behavior which appears to lack integration or organization only because of the frame of reference in which we view it. While the example is not a perfect one, the "integrated" behavior evidenced in the "floundering" of a salamander is equivalent to the "disintegrated" behavior observed in a seizure of "forced movements" in a pigeon. The ability to make specific reactions may be present even though the organization of these specific reactions into functional groups may be absent. The writer has observed a cerebellar bird balance on one leg, lift the other and scratch the back of its neck, during the same observation period in which its gait in walking was greatly impaired. Fearing's data, referred to above, for post-operative behavior in total labyrinthectomies indicate clearly that an animal presenting a generalized picture of severe disturbance at the same time may show many normal specific reactions. Such facts indicate that specific reactions are not completely lost as a result of the cerebellar operation or labyrinthectomy but only "dispersed" with reference to a total functional organization. Focalization of response potentialities has temporarily been abolished. Lashley has made a very similar interpretation of the phenomena of impairment following cerebral lesions in man:

> The symptoms of lesions (cerebral) in man emphasize the dynamic rather than the static in neural organization. There is a simplification of behavior, a reduction in the number of elements which can be dealt with or integrated in a single reaction. This simplification may be so general as to involve almost every aspect of behavior, constituting a general dementia; it may be limited to some one field of activity such as the verbal formulation of propositions or the synthesis of visual impressions; but in every case it affects the majority of reactions of the given type. It is not the specific reaction but the mode of synthesizing activity which is affected by cerebral lesion. Along with this there may go an apparent weakening of the reaction mechanism. Reactions are not absolutely abolished but only rendered difficult, so that some extraneous facilitation is required before they can be elicited. Here also, not specific reactions but groups of reactions are affected and the grouping is determined by such relations as object-name. It seems as though the unit of cerebral organization can be expressed only in terms of relationships among activities, rather than in terms of individual reactions (56, p. 481).

RE-CONSTITUTION AS A "CONDENSATION" OF RESPONSE POTENTIALITIES

The period of re-constitution, during which "normal" patterns reappear and old ones associated with the period of shock disappear, may be interpreted as a process of condensation (focalizing) of response potentialities. There is no evidence that a bird with an extensive cerebellar lesion or without labyrinths is less able to behave in a quantitative sense. Certainly the energy expenditure during a seizure of "forced movements" must equal that for a large segment of "normal" reactions. Murray (65) has pointed out that forced movements in a labyrinthectomized pigeon may tend to follow as part of a sequence of symptom patterns. Fearing has motion pictures which show that re-constitution proceeds in relationship with the immediate environment of a labyrinthectomized animal. Gradual or sudden change in the environment such as removal of the wire cage from around the animal may result in a "re-constitution" of the most violent types of symptoms. Such observations indicate that the period of re-constitution following lesion is not related primarily to "repair of lesion" but rather represents a directional (perhaps with reference to specific relationships in the environment) re-ordering or "condensation" of various reaction potentialities present in the organism. The extent to which re-constitution in the case of various types of lesions is dependent upon the capacity of "previously unused" structures to take over (vicariously) impaired functions is as yet uncertain (cf. Lashley, 55).

A THEORY OF CEREBELLAR FUNCTIONS

We have seen that under conditions such as those of the present investigation, the effect of a cerebellar lesion upon habituation of post-rotational nystagmus is (1) to reduce the susceptibility of this response to modification by means of repeated elicitations, and (2) to impair the retention of an habituation effect established prior to the lesion. The phenomena of modification following repeated elicitation of post-rotational nystagmus were interpreted in terms of the learning process. Data of Lashley and McCarthy were examined concerning the effects of cerebellar lesions upon the maze habit in the white rat. Contrary to the interpretations of these investigators, evidence was found of a marked disturbance of focalized activity with reference to the maze situation associated with cerebellar injury.

In both of the foregoing instances of disturbance associated with cerebellar injury, the impairment may be interpreted in terms of "dispersion" of response potentialities organized along a time axis with reference to a stimulus situation. In the case of our data, this "dispersion" is reflected by a gradual disappearance of the after-nystagmus elicited by rotation; in the case of the maze habit, the "dispersion" is evidenced by a temporal disorganization of "goal-directed" activity. This temporal disorganization is not sufficiently great, however, to preclude actual running of the maze (witness the fact that the rats did get through). These considerations suggest that the cerebellum is somehow concerned with the temporal ordering of activity. The temporal sequence of responses made with reference to a stimulus situation constitutes, we believe, the common matrix of all acts usually designated as "intelligent behavior." Within wide limits, the differential between an "intelligent" and an "un-intelligent" animal is not to be found in terms of ability to act in a quantitative sense. The superior "intelligence" of the one reflects a capacity for higher degrees of functional organization, i.e., temporal ordering of activity such that the *response-as-a-whole* to a stimulus situation is, in terms of the goal, appropriate. Damage to the cerebellum impairs this activity of the central nervous system; thus the cerebellum must play an important rôle in so-called "intelligent" behavior.

But what of the rôle of the cerebral cortex in such processes? Lashley has reported a coefficient of correlation of .86 (P.E. .03) between the mass of cortical tissue destroyed and post-operative re-learning of an eight culs de sac maze (54a). Learning was measured in terms of errors made in satisfying the criterion of "10 consecutive errorless trials." As Lashley points out (56), this high relationship between impairment and mass tissue is probably related to greater change in some "central dynamic state." Contrary to the contention of Lashley and others that this "central dynamic state" represents more or less autonomous functioning of the cerebral cortex, the suggestion is presented that (1) the "central dynamic state" always involves the cerebrum and the cerebellum, (2) for certain types of "higher" activities the cerebellum may contribute the dominant component. Relationships which have so far been described in the literature as dependent upon cortical activity may also be described as dependent upon cerebellar activity.[15] As a schematic represen-

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[15] Among neurologists, Herrick has emphasized the reciprocal relationship between the cerebellum and the cerebral cortex. In the fifth edition (1931) of his *Introduction to Neurology* he wrote:

"The axons of the Purkinje cells (in the cerebellum) themselves also give off collateral fibers into the granular layer, whose neurons discharge back into the Purkinje cells again. In . . . these ways provision is made for the diffusion, summation, and reinforcement of stimuli during the process of their transmission through the cerebellar cortex, and also for prolongation of motor reactions which tation of possible cerebellar-cerebral relationships we offer the following example. Let us imagine a fleet of warships undergoing maneuvers that are being controlled by radio beacons sent out from a battery of stations located on the shore. For successful consummation of the maneuvers, precise ordering of the spatial (or temporal) relationship of each ship to every other ship in the total configuration is demanded. Barring internal mechanical defects, there are two ways in which such a directed configuration might be disturbed from without: (1) disturbance in the region of the sending stations located on the shore (cerebellum), (2) disturbance in the region of the fleet (cortex). In case of the latter, damage to the radio antenna of one ship might result in sufficient disturbance of the total configuration as to greatly alarm the Admiral observing from his flagship; to observers getting an airplane-view of the situation, no evidence of the trouble below might appear. Loss of the antenna of three or four ships would doubtless so disrupt the maneuver that the aerial observers would note the signs of confusion. In observing they might even have noticed the very close correspondence between the number of antennae destroyed or damaged and the increasing disturbance of the fleet configuration as it appeared from below.[16]

In suggesting this theory of cerebellar activity we have taken cognizance of the following lines of evidence: (1) phylogenetically, the cerebellum and the cerebrum develop in parallel manner, (2) physiological studies suggest intimate functional relationship between these two structures, (3) two of the three major components of the cerebellum are related anatomically, via its peduncles, to the cerebrum, (4) studies such as the present which touch upon the physiology of learning indicate that the cerebellum is involved in learning processes.

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would otherwise soon subside. . . . It is probable that the reciprocal relation between the cerebellum and the cerebral cortex is of a similar sort, all cortical activities exciting also the cerebellum and drawing therefrom additional nervous energy as needed . . ." (p. 228).

[16] It would be possible, of course, to extend our example to illustrate the redintegrating circuits by which the cerebellum and cerebrum are probably related physiologically.

CHAPTER XV

General Summary

As stated previously, the purpose of the present investigation was threefold: (1) it was desired to determine whether the phenomena commonly designated as habituation, which results from repeated elicitation of post-rotational nystagmus, is a process involving a modification within the central nervous system; (2) it was desired to determine the effects of cerebellar lesions upon the habituation of post-rotational nystagmus; (3) it was desired to adduce evidence concerning the nature of cerebellar functions. In the foregoing pages evidence has been presented which indicates that (1) habituation is probably a "central" phenomenon, (2) the cerebellum is directly involved in the habituation process as considered herein, and (3) under appropriate conditions the cerebellum may function directly in a process which may be interpreted as "learning." Explicit statement of the various findings is made below.

(1) Systematic observation of the behavior of birds with cerebellar lesions revealed the fact that marked "recovery" usually takes place within a two-week period following the operation. The post-operative behavior was considered in terms of three periods: (1) a period of shock, characterized by severe disturbance, (2) a period of re-constitution, characterized by reappearance of "normal" behavior patterns and disappearance of behavior associated with period of shock, and (3) a period of redintegration, during which a structurally modified organism may exhibit all of the behavior patterns of a "normal" animal.

(2) When after a period of from four months to one year following a cerebellar operation a number of birds were tested for duration of post-rotational nystagmus, such birds were found to exhibit nystagmus times characteristic of normal animals. In other words, the cerebellar lesion neither increased nor decreased the duration of after-nystagmus.

(3) In all animals, successive elicitation of after-nystagmus over a period either of ten or of fourteen days resulted in the usual modification

of the response in the direction of extinction. This reduction or habituation effect, under conditions of the present investigation, was found to range between 50 and 60 per cent of the original duration of after-nystagmus. Both cerebellar and control animals exhibit this habituation effect. However, with the same amount of rotational experience, the habituation effect is significantly less in the case of birds with cerebellar lesions. Differences in favor of greater degree of habituation in the normal animals is of the order of 2.5:1.

(4) When tested after a two-week interim without rotational experience two groups of habituated birds, directly comparable (except that one group had a cerebellar operation following habituation), showed marked difference in average duration of post-rotational nystagmus. Whereas the cerebellar group had lost approximately half of the habituation effect, the control group showed no loss. Similar findings were noted in a group comparable in all respects to the above with the exception that the nystagmus tests were made after an interim of four instead of two weeks.

(5) Control experiments revealed the effect of the anaesthesia (Nembutal) and the auditory component of the stimulus situation (hum of motor associated with starting and stopping of rotator) to be neutral as far as differential habituation between operated and control groups is concerned.

(6) Attempts to re-establish the pre-operative level of habituation in the case of two birds failed for a five-day period of successive rotations. Habituation was noted in the records for a given day in practically every instance, however. This suggests that failure to re-habituate was due to failure to retain and thus to accumulate the increment of habituation effect contributed by each day of successive rotations.

(7) Stop watch latencies for the quick component of after-nystagmus revealed no evidence of any consistent change associated with the total habituation process. Some relationship between length of the latent period and degree of habituation was noted for the first few days of the habituation period, however.

(8) A significant degree of habituation was found to persist both in control and cerebellar animals for as long as three months after the end of the habituation period. Between three and four weeks after the end of the habituation period all animals began to exhibit a gradual loss of habituation effect. The end-point for complete loss is somewhere beyond three months in the case of pigeons.

(9) It was found that habituation by rotation in one direction may be

expected to transfer almost completely (both for operated and control birds) to the "unpracticed" direction, under the conditions and time intervals employed in the present investigation.

(10) Histological analysis was made of all operated and some control animals. It was found that the lesions ranged from approximately 20 to 80 per cent of the total volume of the cerebellum with 40 per cent as the average percentage of destruction. The lesions, placed bilaterally to the mid-line by means of a thermo-cautery, invaded principally the anterior and middle lobes of the cerebellum in each instance. With the exception of one animal, see (11) below, no evidence was found of extra-cerebellar involvement associated with the lesions.

(11) The records of an animal having both a cerebellar lesion and damage to underlying vestibular structures were analyzed separately. This animal exhibited an original after-nystagmus time approximately 300 per cent that of either cerebellar or control animals. It habituated like normal animals; but by the end of a three-month period it had lost more than 100 per cent of the habituation effect. The possible clinical significance of this fact was indicated.

(12) In interpreting the rôle played by the cerebellum in the above relationships, the phenomena of habituation were compared with phenomena generally regarded as "learning." This comparison led to the conclusion that the habituation process, as herein considered, is of the nature of learning. Since damage to the cerebellum was shown to retard the learning process or to impair retention, it was also concluded that the cerebellum participates directly in learning situations.

(13) It was found that traditional theories of cerebellar function are inadequate to account for the phenomena described in (12). Accordingly, a theory of cerebellar function was proposed which holds, that (1) theories which attempt to account for the so-called "higher processes" in terms of autonomous cortical mechanisms are in error, (2) the "central dynamic state" as proposed by Lashley always involves the cerebellum and cerebrum rather than just the latter structure as claimed by Lashley and others, (3) for certain types of "higher" activities the cerebellum may contribute the dominant component.

CHAPTER XVI

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Vol. 12 No. 2 JANUARY, 1936 Serial No. 57

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THE FUNCTIONS OF THE VISUAL AREAS OF THE CEREBRAL CORTEX OF THE RAT IN THE LEARNING AND RETENTION OF THE MAZE. II

BY
YÜ-CHÜAN TSANG
The University of Chicago

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THE FUNCTIONS OF THE VISUAL AREAS OF THE CEREBRAL CORTEX OF THE RAT IN THE LEARNING AND RETENTION OF THE MAZE. II[1]

YÜ-CHÜAN TSANG

The Department of Psychology, The University of Chicago

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[1] The writer wishes to acknowledge his profound gratitude to Professor K. S. Lashley for constant encouragement and invaluable advice throughout this research.

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PROBLEM RESTATED AND PRELIMINARY RESULTS SUMMARIZED

In the first part of this study (Tsang, '34) we set out to answer the question, whether the visual areas of the cerebral cortex are purely sensory in function, or they have some non-sensory functions besides visual reception. This is one aspect of the broader question whether or not the cortical sensory projection areas have non-sensory functions. In our experimental attack we first compared the learning scores of the normal and peripherally blinded rats for the inclosed and the open mazes of same pattern. The peripherally blinded were found to be close matches of the normals in the inclosed maze, but they were much inferior to the latter in the open maze. Vision is not essential for learning the inclosed maze, while its rôle in the open problem is very great. We next determined the influence of the removal of the visual areas upon efficiency in the maze. The logic of this procedure is the following: if the visual cortex is merely visual in function, the retardation in learning following its destruction should be proportional to the use of vision in the two mazes. But, as a matter of fact, we found that cortical destruction limited to the visual areas had a disproportionately greater effect in the inclosed maze in which vision is scarcely used. Moreover, the retardation in maze learning was in general greater after lesions in the visual cortex than after peripheral blinding. The loss of the "cortical retinae" was much more detrimental than the loss of the peripheral retinae. We then concluded that the visually specialized cortex has some important general, non-sensory functions in addition to visual reception.

The nature of this function remains obscure. It may be, as Lashley has suggested, one of facilitation of other nervous centers, a contribution to the general level of central nervous tones. But it is also possible that the non-sensory function is a specific one, closely related to visual reception.

Our animals were adults which had free use of vision until the

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beginning of the experiments. They might, therefore, have developed a system of visual habits which could serve as a frame of reference for spatial orientation. Such a spatial system organized in visual terms (visual images?) might survive peripheral blinding but be destroyed by lesions in the visual cortex. Thus the disturbance of the maze function in peripherally blinded animals by lesions in the striate cortex is not conclusive evidence for a non-visual function of the striate cortex, although it does indicate something more than a "perceptual" function.

The present experiments were designed to test the function of the striate cortex in animals which had been prevented from forming any visual-space habits by blinding at birth. If the activity of the visual cortex is restricted to learned visual functions (sensory and imaginal), then the behavior of animals blinded from birth should be the same, with or without the visual cortex.

We removed the eyes from the animals on the thirteenth day, just before they open naturally. The visual system was thus prevented from any stimulation which would give rise to the formation of spatial habits. The blinded animals were divided into two groups, one for tests of initial learning, the other for post-operative retention tests. With the first group we wished to determine whether absence of the striate areas would have a retarding influence on maze learning above that resulting from peripheral blindness alone; with the second group to determine whether or not the striate cortex participated in maze learning in animals blind from birth. This should be a more crucial test for the non-visual functions of the striate cortex.

METHOD AND PROCEDURE

The experimental procedure was essentially the same as for Part I, to which the reader is referred for details. We shall state briefly a few points not covered therein, or of which a clear presentation of the results demands a repetition.

1. *Mazes*

The same inclosed and open mazes of same pattern were used. They consisted of fifteen sections, eight being culs-de-sac. The sequence of correct turns from the starting to the feeding box is *rllrrllr*.

2. Animal Groups

One hundred and one hooded rats were employed. They were born in the laboratory in which they were trained afterwards. All of them were blinded by enucleation of eyes on the thirteenth day. For the experiment on initial learning in the absence of striate areas, 22 blind rats were used as controls and 25 were subjected to destruction of the striate areas at about 3 months of age. These groups were each divided equally for first training on the open or inclosed maze.

For postoperative retention tests 44 blind animals were trained in the two mazes. Twenty-two of them were then subjected to destruction of the striate areas and all were later tested for retention of the maze habit.

We then have eight subgroups of animals for comparison:

Initial learning tests

Subgroup ILa. Peripherally operated, first ran inclosed, then open, maze.
Subgroup ILb. Peripherally operated, first ran open, then inclosed, maze.
Subgroup IILa. Combined operation, first ran inclosed, then open, maze.
Subgroup IILb. Combined operation, first ran open, then inclosed, maze.

Postoperative retention tests

Subgroup IRa. Peripherally operated, learned and relearned inclosed maze.
Subgroup IRb. Peripherally operated, learned and relearned open maze.
Subgroup IIRa. Combined operation, learned and relearned inclosed maze.
Subgroup IIRb. Combined operation, learned and relearned open maze.

The normal Subgroups Ia (inclosed maze) and Ib (open maze) of Part I were used as controls for the initial learning groups.

3. Training

Training of the animals began around 100 days after birth. For the learning groups we followed strictly the procedure of Part I. Hunger was used as incentive to learning. The length of feeding time was controlled. We adopted the usual criteria of learning, time spent, errors made and trials taken. The error scores are stressed in the interpretation of results because of their generally acknowledged high reliability. Ten consecutive errorless runs was the criterion of mastery for a maze problem. One hundred and fifty trials was the maximum allowed each animal. The animals were first trained in one maze and then transferred to the other. Thus, one maze served as the first problem for one subgroup and as the second problem for the other.

For the learning and relearning of the retention groups no arbitrary number of trials was set; they were trained until the standard of proficiency was attained. Upon completion of the initial learning, Subgroups IRa and IRb were rested in the home cage for the following two weeks on the same ration as during training. With Subgroups IIRa and IIRb, the operation on the visual cortex was made immediately following the completion of initial learning.

4. Surgical and Neurological Techniques

Under ether anesthesia the eyelids of the pups were separated by a needle. The eye-ball was held between curved wire-forceps and cut off with small dissecting scissors. The visual areas of the adult animals were removed under deep anesthesia with an electric thermocautery. We at first followed the procedure of Part I and destroyed the projection as well as the supposed association areas, that is, Fortuyn's ('11) areas w and m′ and aa (see fig. 2, Part I). But we soon limited the operation to the projection areas alone. For animals in the learning groups ten days were allowed for recovery from the operation; for those to be tested for postoperative retention the two weeks's retention period allowed time for recovery.

The brains of animals with cerebral lesions were removed upon completion of learning or relearning and prepared for sectioning. Celloidin sections of 40 μ were cut and stained with thionin. On the basis of representative sections taken at definite intervals, the brain lesion was reconstructed for each case on Lashley's diagram of rat's cerebrum. The size of the lesion was measured on the diagram and expressed as the percentage of the surface area of the neopallium.

TABLE I

Individual Records of Learning of the Inclosed and the Open Mazes by the Peripherally Blinded Animals

Subgroup ILa ran first the inclosed and then the open maze; Subgroup ILb ran first the open and then the inclosed maze. Total time, total errors and total trials preceding the ten consecutive errorless trials, or on the completion of the arbitrary number of one hundred and fifty trials at which training was discontinued, are given for each animal.

ANIMAL GROUP	NUMBER	SEX	INCLOSED MAZE			OPEN MAZE		
			Time	Errors	Trials	Time	Errors	Trials
			seconds			*seconds*		
ILa	1	f	246	18	11	1,753	161	55
	4	m	2,704	167	106	1,687	110	150 (82)*
	8	m	831	31	12	1,125	60	83
	36	m	788	58	31	894	37	24
	49	f	5,846	315	150 (72)	1,267	72	38
	50	m	2,622	137	122	1,899	110	78
	65	f	1,383	58	44	2,035	120	84
	66	f	964	47	31	1,635	107	77
	74	f	1,516	123	93	1,438	57	41
	83	f	1,509	110	25	2,008	115	23
	86	f	2,731	168	125	874	46	41
ILb	2	f	712	60	77	3,297	228	150 (79)
	5	m	335	26	14	2,762	140	78
	9	m	329	20	10	3,093	173	61
	12	m	582	26	26	2,181	114	150 (87)
	33	f	1,814	122	150 (93)	5,063	329	150 (58)
	48	f	553	52	26	9,096	574	150 (48)
	53	m	993	61	68	8,102	360	150 (42)
	69	f	231	8	30	5,550	249	95
	70	f	713	38	72	11,856	373	150 (57)
	73	f	1,745	108	150 (83)	2,968	162	107
	95	f	912	57	67	2,585	106	41

* Figures in parentheses are errorless trials.

The reconstructions of the brain lesions are given in the plates at the end of this report. Only dorsal views of the lesions are

TABLE II

Individual Records of Learning of the Inclosed and the Open Mazes by Animals Both Peripherally and Cortically Operated

The percentage of the total neopallium destroyed is given at the left. Brain diagrams illustrating the lesions are given under corresponding numbers in the plates at the end of this report. Subgroup IILa ran first the inclosed and then the open maze; Subgroup IILb ran first the open and then the inclosed maze. Total time, total errors and total trials preceding the ten consecutive errorless trials, or on the completion of the arbitrary number of one hundred and fifty trials at which training was discontinued, are given for each animal.

ANIMAL GROUP	NUMBER	SEX	PERCENTAGE OF LESION	INCLOSED MAZE			OPEN MAZE		
				Time	Errors	Trials	Time	Errors	Trials
				seconds			*seconds*		
IILa	11	m	17.4	6,113	321	105	2,320	168	150 (81)
	13	f	16.0	3,394	250	135	3,079	309	150 (50)
	18	m	10.2	1,115	93	22	858	49	44
	19	m	24.2	1,186	135	74	2,083	227	150 (84)
	24	m	17.8	4,347	215	108	3,232	226	116
	32	f	14.7	1,868	146	73	5,456	557	150 (47)
	41	m	18.5	3,628	358	136	2,581	259	127
	46	m	21.1	3,117	262	109	4,088	381	150 (28)
	59	f	20.0	1,687	190	53	4,410	400	150 (30)
	91	f	21.1	1,680	200	49	5,414	385	150 (52)
	100	f	12.4	14,725	1,189	134	17,084	1,543	150 (3)
	103	f	12.5	20,181	1,081	150 (37)	20,768	626	150 (42)
IILb	22	m	17.4	786	62	8	1,772	127	29
	27	m	17.0	424	20	24	6,628	134	116
	31	f	22.5	2,016	122	98	3,414	451	150 (50)
	34	f	23.2	975	65	38	3,620	602	150 (37)
	38	m	14.0	706	38	27	4,574	329	104
	43	m	18.9	2,539	104	26	19,036	766	150 (38)
	44	m	16.0	905	82	67	5,351	333	121
	45	m	19.1	1,289	59	69	6,253	559	150 (19)
	55	m	21.1	656	57	25	7,101	559	150 (35)
	56	m	19.8	687	86	32	2,714	468	150 (37)
	76	f	15.3	397	26	7	6,177	368	139
	90	f	20.9	2,142	193	122	3,837	447	150 (47)
	104	f	10.6	14,292	1,141	150 (18)	41,753	3,975	150 (0)

shown. For the few cases with extensive lesions the lateral views of the wounds were also reconstructed for measurement but not shown in the plates.

TABLE III

Comparison of the Average Learning Scores of Normal Controls and of Animals Operated Peripherally and Both Peripherally and Cortically for the Mazes When They Were Either Their First or Second Problems

The averages are based upon all cases in each group which reached the criterion of learning or completed the arbitrary number of one hundred and fifty trials. The group average scores of the peripherally operated for the mazes when they were their first problems were calculated by averaging together the gross learning scores of Subgroup IL (a or b) of the learning group proper and those of Subgroups IR (a or b) and IIR (a or b) of the retention group, which with then a peripheral operation also ran the maze as their first task. The average percentage of cerebral lesions is given for each cortically operated subgroup. Averages of time, errors and trials are given together with their respective probable errors. Under "Difference" the absolute difference between the normal and the operated subgroups is given; under "Percentage" the absolute difference is expressed as the percentage of the corresponding average of the normal subgroup; and under "Average Retardation" the average of the three percentage differences is presented.

	ANIMAL GROUP	NUMBER OF CASES	AVERAGE PERCENTAGE OF LESIONS	CRITERIA	AVERAGE SCORES	DIFFERENCE	PERCENTAGE	AVERAGE RETARDATION
				For the Inclosed Maze				
As 1st Problem	Ia (Normal)*	11		Time	2,338.00 ± 449.67			
				Errors	98.82 ± 14.44			
				Trials	38.18 ± 4.86			
	ILa (IRa and IIRa) (Peripherally operated)	37		Time	2,047.00 ± 195.22	−291.00	−12.45	20.88
				Errors	107.51 ± 9.85	8.69	8.79	
				Trials	63.49 ± 4.46	25.31	66.29	
	IILa (Peripherally and cortically operated)	12	17.2	Time	5,253.00 ± 1,119.07	2,915.00	124.68	183.23
				Errors	370.00 ± 68.28	271.18	274.42	
				Trials	95.67 ± 7.64	57.49	150.58	

As 2nd Problem	Ib (Normal)*	11		Time Errors Trials	948.00 ± 147.95 61.00 ± 8.49 37.82 ± 3.97			
	ILb (Peripherally operated)	11		Time Errors Trials	811.00 ± 103.45 52.55 ± 6.91 62.73 ± 9.58	−137.00 −8.45 24.91	−14.45 −13.85 65.86	12.52
	IILb (Peripherally and cortically operated)	13	18.1	Time Errors Trials	2,140.00 ± 666.88 158.08 ± 53.64 53.31 ± 8.11	1,192.00 97.08 15.49	125.74 159.15 40.96	108.62
For the Open Maze								
As 1st Problem	Ib (Normal)**	11		Time Errors Trials	2,194.00 ± 297.08 74.91 ± 9.14 34.55 ± 3.57			
	ILb (IRb and IIRb) (Peripherally operated)	38		Time Errors Trials	4,705.00 ± 322.37 243.66 ± 17.80 110.03 ± 5.31	2,511.00 168.75 75.48	114.45 225.27 218.47	186.06
	IILb (Peripherally and cortically operated)	13	18.1	Time Errors Trials	8,633.00 ± 6,148.92 701.38 ± 179.44 131.46 ± 6.22	6439.00 626.47 96.91	293.48 836.30 280.49	470.09
As 2nd Problem	Ia (Normal)**	11		Time Errors Trials	1,128.00 ± 217.56 50.64 ± 8.76 28.73 ± 5.49			
	ILa (Peripherally operated)	11		Time Errors Trials	1,510.00 ± 82.01 90.45 ± 7.43 63.09 ± 7.14	382.00 39.81 34.36	33.87 78.61 119.60	77.36
	IILa (Peripherally and cortically operated)	12	17.2	Time Errors Trials	5,948.00 ± 1,168.18 427.50 ± 72.05 136.42 ± 5.82	4,820.00 376.86 107.69	427.30 744.19 374.83	515.44

* Scores taken from Table V (Tsang, '34).

** Scores taken from Table VI, *ibid.*

EFFECTS OF PERIPHERAL AND CORTICAL OPERATIONS UPON INITIAL LEARNING SCORES

1. Experimental Data

The individual records of learning of the mazes by animals peripherally blinded in infancy are given in Table I. Subgroup ILa was first trained in the inclosed and then transferred to the open maze; Subgroup ILb was first trained in the open and then transferred to the inclosed maze. Total time spent, total errors made and total trials taken preceding the ten consecutive errorless trials or within 150 trials in case of failure, are given for each animal.

In Table II are shown the individual learning scores of animals peripherally blinded in infancy and deprived of visual areas at adult age before training. The percentage of the total neopallium removed in each case is given. Subgroup IILa ran first the inclosed and then the open maze; Subgroup IILb ran first the open and then the inclosed maze. Time, error and trial scores are given for each case.

Additional data on initial learning of peripherally blinded animals are given by the preoperative training of the groups (IRa and b, IIRa and b) used for tests of postoperative retention. Their individual learning scores are given in Table VI. For a comparison of the blind groups with normal animals the records from our first report are available (Table I, Part I). These are included in Table III as Subgroups Ia and Ib.

The averages of initial learning scores have been computed for the differently treated groups and are presented in Table III. The scores of animals which failed to learn the maze in 150 trials were averaged together with the successful cases of the same subgroup. The differences between the scores of the operated animals and the normal ones (Subgroups Ia and Ib) have been computed and expressed as percentages of the normal scores. The averages of these percentages for the different criteria of learning are given in the last column.

2. Effects of Peripheral Blinding on the Learning of the Mazes

Comparing the scores of normal and peripherally blinded animals in Table III we find that the effects of blinding in infancy differ for the inclosed and the open mazes, just as they did in our study of animals blinded at adult age. We shall treat the mazes separately:

a. Inclosed Maze. In the inclosed maze blind animals do almost as well as normals. The peripherally blinded Subgroups ILa and ILb ran the inclosed maze as their first and second problem respectively. The time, error and trial scores of these animals for the inclosed maze are close to the normal scores, some of them being even better (Table III). The differences in the scores are generally not much greater than the chance deviations of the normal scores. Let us compare their error scores for the mazes:

SUBGROUP	PROBLEM	ERROR SCORE	DIFFERENCE
Ia (Normal)	Inclosed maze, first	98.82 ± 14.44	8.69 ± 17.48
ILa (Peripherally operated)	Inclosed maze, first	107.51 ± 9.85	
Ib (Normal)	Inclosed maze, second	61.00 ± 8.49	−8.45 ± 10.95
ILb (Peripherally operated)	Inclosed maze, second	52.55 ± 6.91	

We see that the differences in the error scores of the blind and normal animals are within the limits of the probable errors of the latter. The average retardation of Subgroup ILa, based on all criteria, is 20.88 per cent and that of Subgroup ILb, 12.52 per cent. This amount of retardation is statistically not very important in comparison with that following cortical operation to be presented below. We averaged these two together and arrived at a combined retardation of 16.70 per cent for the peripherally blinded in the inclosed maze. Thus, the effects of peripheral blinding on the learning of the inclosed maze is very slight.

b. Open Maze. The situation in the open maze is quite different. The average scores of the blind rats for the three criteria are invariably poorer than the corresponding normal scores (Table III). We again take up the error scores for the open maze of the peripherally blinded Subgroups ILb and ILa which ran this maze as the first and second problem respectively and compare them with the error scores of the normals:

SUBGROUP	PROBLEM	ERROR SCORE	DIFFERENCE
Ib (Normal)	Open maze, first	74.91 ± 9.14	168.75 ± 20.01
ILb (Peripherally operated)	Open maze, first	243.66 ± 17.80	
Ia (Normal)	Open maze, second	50.64 ± 8.76	39.81 ± 11.49
ILa (Peripherally operated)	Open maze, second	90.45 ± 7.43	

The blind animals made many more errors than the normals in the open maze. The average retardation for all criteria of Subgroups ILb and ILa are 186.06 and 77.36 per cent respectively (Table III). The average of these two is 131.71 per cent. The blind animals are thus more than twice as poor as the normals in the open maze.

Summing up, peripheral privation of vision has little effect on the learning scores for the inclosed maze (16.70 per cent), but it exerts tremendous influence on the learning of the open maze (131.71 per cent). The greater rôle of vision in learning the open maze is thus once more demonstrated.

We are now to test the functions of the visual areas in the learning of the mazes. If these areas are purely visual in function, their elimination in animals blind from birth should have no effect on maze efficiency beyond that following the peripheral blinding.

3. *Effects of Cortical Operation on the Learning of the Mazes*

a. Inclosed Maze. The inferiority of the animals with cortical lesions to the peripherally operated ones in the inclosed maze is evident from a comparison of the average scores of Subgroups IILa and ILa (Table III) which ran this maze as the first problem. The cortically operated Subgroup IILa spent more time, made more errors and took more trials than the peripherally blinded Subgroup ILa. Their error scores are tabulated below:

SUBGROUP	PROBLEM	ERROR SCORES	DIFFERENCE
ILa (Peripherally operated)	Inclosed maze, first	107.51 ± 9.85	262.49 ± 68.99
IILa (Peripherally and cortically operated)	Inclosed maze, first	370.00 ± 68.28	

The cortically operated made more than three times as many errors as the peripherally operated. By all criteria they show a retardation of 183.23 per cent, their score being nine times that of Subgroup ILa (20.88 per cent) as shown in Table III.

Similarly, the cortically operated Subgroup IILb which ran the inclosed maze as the second problem was much inferior to the peripherally operated Subgroup ILb in the same maze. We reproduce their error scores below:

SUBGROUP	PROBLEM	ERROR SCORE	DIFFERENCE
ILb (Peripherally operated)	Inclosed maze, second	52.55 ± 6.91	105.53 ± 53.08
IILb (Peripherally and cortically operated)	Inclosed maze, second	158.08 ± 53.64	

Subgroup IILb made three times as many errors as Subgroup ILb. The difference in the time scores is in the same direction. The trial score deviates from the general tendency. The average retardation of Subgroup IILb for all criteria is 108.62, being also nine times that of the peripherally blinded Subgroup ILb (12.52 per cent).

The combined retardation of the cortically operated Subgroups IILa and IILb for the inclosed maze is 145.93 per cent, while that of the peripherally blinded Subgroups ILa and ILb is 16.70 per cent, a ratio of 9 to 1.

b. Open Maze. A similar contrast exists in the records of the peripherally and cortically operated animals for the open maze. The striking inferiority of the cortically operated is amply shown by comparing the average scores of Subgroup IILb, thus operated, with the corresponding scores of Subgroup ILb, peripherally operated, for the open maze, which was their first problem. We take up their error scores.

SUBGROUP	PROBLEM	ERROR SCORE	DIFFERENCE
ILb (Peripherally operated)	Open maze, first	243.66 ± 17.80	457.72 ± 180.32
IILb (Peripherally and cortically operated)	Open maze, first	701.38 ± 179.44	

The cortically operated group is almost three times poorer than the peripherally operated, as judged by the error scores. The former also spent more time and required more trials. The average scores of Subgroup IILb may seem too much influenced by the poor records of No. 104. The operation in this animal is one of ideal type, however, with lesion strictly limited to the striate cortex, so this case should be included in calculating the group constants. If it is omitted, the contrast between animals with peripheral and combined operation still remains, but is not so great. Sixty one per cent of Subgroup IILb failed the open maze, whereas the corresponding percentage of Subgroup ILb is 47.4. The average retardation of Subgroup IILb based on all criteria amounts to 470.09 per cent, in contrast to the 186.06 per cent of Subgroup ILb.

In even sharper contrast we find the scores of the cortically operated Subgroup IILa and the peripherally operated Subgroup ILa for the open maze run as their second problem. Their error scores are reproduced below:

SUBGROUP	PROBLEM	ERROR SCORE	DIFFERENCE
ILa (Peripherally operated)	Open maze, second	90.45 ± 7.43	337.05 ± 72.43
IILa (Peripherally and cortically operated)	Open maze, second	427.50 ± 72.05	

The error score of the cortically operated is more than four times that of the peripherally operated. The time and trial scores of the former are also much higher. No less than 75.0 per cent of the animals in Subgroup IILa failed to learn the maze in 150 trials; whereas the corresponding percentage of Subgroup ILa is merely 9.1. The average retardation of Subgroup IILa runs as high as 515.44 per cent, whereas that of Subgroup ILa is 77.36 per cent.

The cortically operated Subgroups IILb and IILa give a combined retardation of 492.77 per cent for the open maze, and the corresponding constant for the peripherally operated Subgroups ILb and ILa is 131.71 per cent, a ratio of 4 to 1.

Thus, the cortical operation has much greater retarding effects on the learning scores than the corresponding peripheral operation. This is true for both the inclosed and the open mazes, run either as the first or the second problems. The disproportionately greater influence of the removal of the visual areas implies that these areas have additional functional significance, besides that of visual reception or any other visual function which is acquired as a result of visual experience.

4. Summary of Data on Learning

The average retardations of the animal groups with peripheral or combined operation for the mazes are represented by horizontal bars in Figure 1. The length of the bars is proportional to the degree of retardation in terms of the percentage of the normal group scores for the same problems. The upper part of the histogram illustrates the retardations of the differently operated animal groups for the mazes run as the first problems. The middle part shows the retardations for the mazes run as the second problems. The lower part presents the averages of the upper two, showing the combined retardations of similarly operated animal groups. It is clear that in the three pairs of group comparisons the same sharp contrast prevails: the cortically operated are invariably more retarded than the peripherally operated.

We shall sum up in a few lines the results on the learning of the mazes by the various animal groups. Animals peripherally blinded in infancy are almost as good as normals in the inclosed maze. With the additional removal of the visual areas they are seriously retarded in learning the same problem. The facts are essentially the same for the open maze, yet the contrast is not so sharp, owing chiefly to the fact that the open maze habit is primarily a visual affair and the peripheral blinding tremendously interferes with its formation. It is the additional effect of the cortical operation that is significant for interpreting the function of the visual cortex.

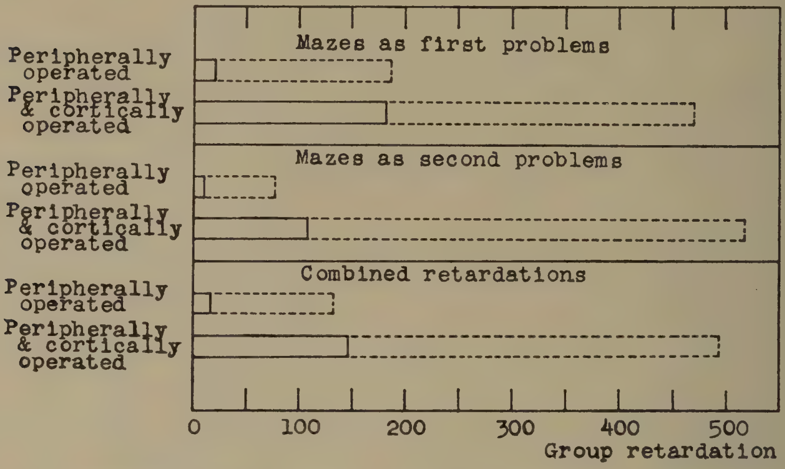

FIG. 1. HISTOGRAM OF THE AVERAGE RETARDATIONS FOR THE MAZE PROBLEMS OF THE DIFFERENTLY OPERATED ANIMAL GROUPS
——— inclosed maze; ---------- open maze

5. Possible Influences of Additional Subcortical and Non-striate Cortical Injuries on Learning Scores

In many of the cortically operated animals the lesions covered more than the strictly visual cortex—the striate area. The hippocampus was touched very often, as the visual area is the thinnest part of the whole neopallium, and it is especially difficult to avoid the underlying structures completely when the electric thermocautery is used for the destruction. In a few cases the superficial parts of thalamus and tectum were injured slightly. The greater retardation following cortical operation might then be a consequence of the involvement of such non-visual extrastriate structures and it is necessary to control our results by investigating the possible effects of such additional injuries.

TABLE IV

Comparison of the Error Scores of Learning of Animals with and without Subcortical Lesions in Addition to the Removal of Visual Areas for the Inclosed and Open Mazes Which Were Their First Problems

Under "Effect" the apparently positive (+) or negative (−) influence of the subcortical lesions upon the error score is indicated.

ANIMAL GROUP	KIND OF LESION	WITH SUBCORTICAL LESION				WITHOUT SUBCORTICAL LESION			EFFECT
		Cases (experimental numbers)	Number of cases	Average percentage lesion	Average error score	Number of cases	Average percentage lesion	Average error score	
IIIa, Inclosed Maze	Thalamic	59, 91	2	20.6	195.00	10	16.5	405.00	−
	Mesencephalic	46	1	21.1	262.00	11	16.8	379.82	−
	Hippocampal:					4			
	Light	13, 24	2	16.9	232.50	(11, 18, 100, 103)	13.1	671.00	−
	Extensive	19, 32, 41, 46, 59, 91	6	19.9	215.17				
IIIb, Open Maze	Thalamic	34	1	23.2	602.00	12	17.7	378.42	+
	Mesencephalic	31, 90	2	21.7	449.00	11	17.5	385.91	+
	Hippocampal:					6	15.7	944.00	−
	Light	31, 45, 55, 56, 76	5	19.6	481.00	(22, 27, 38, 43, 44, 104)			
	Extensive	34, 90	2	22.1	524.50				

a. Possible Influences of Subcortical Injuries. In Table IV we compare the error scores of the cortically operated animals with and without subcortical lesions for the mazes run as their first problems. The conditions in the learning of the first maze are undoubtedly simpler than those in the second problem. The reliability of the error score is generally acknowledged as the highest among the criteria of learning. The subcortical injuries fall roughly into three classes: thalamic, mesencephalic and hippocampal. We compare animals with each type of injury with those without such lesions in the same experimental group, neglecting for the time being other subcortical injuries than those under consideration. In this way we hope to get some insight into the possible influence of a subcortical lesion upon the group scores. We see from the table that animals with additional thalamic, mesencephalic or hippocampal injuries made no more errors in the inclosed maze than those without. There have been calculated six error scores for the various classes of animals in Subgroup IILa with or without each type of subcortical injury, viz., 195.00 vs. 405.00; 262.00 vs. 379.82; 223.84 (the two scores of the classes with light and extensive hippocampal injuries are averaged) vs. 671.00. The six scores are all much higher than that of the peripherally blinded Subgroup ILa, 107.51. The error score for the group without a given subcortical lesion is in each case higher than that for the group with the subcortical injury.

In the open maze, animals in Subgroup IILb with thalamic or mesencephalic injury made more errors than those without. Animals with hippocampal injuries, on the contrary, were markedly superior to those without. The three pairs of constants are the following: 602.00 vs. 378.42; 449.00 vs. 385.91; 502.75 vs. 944.00. Since the groups with subcortical lesions are small, these differences are not statistically significant. In no case does the elimination of animals with a given type of subcortical lesion reduce the error score to that of the peripherally blinded control group ILb which is 243.66. It is thus clear, from the scores of both the inclosed and the open mazes, that the retardation following cortical lesions is not due to any chance injury to subcortical structures, but is a consequence of the destruction of the cortex itself.

b. Possible Influences of Non-striate Cortical Lesions. We at first destroyed intentionally the supposed visual association areas m′ and aa, in addition to the striate area w. Other areas adjacent to area w, i.e., auditory area p, somesthetic area j and motor areas f′ and n, were frequently invaded by the operations. The invasion of these surrounding areas was in most cases slight, of a magnitude which, without the striate lesion, has been shown by Lashley to have little if any effect upon maze learning. Nevertheless, since the slight invasion of the somesthetic or other non-visual areas might produce some retardation of maze learning, the influence of such lesions must be controlled before we can draw conclusions concerning the functions of the striate areas. Among our cases there are several in each group with the lesions definitely limited to the striate areas. The limits of these lesions have been established both by plotting the surface extent in comparison to that of the striate areas and also by a careful survey of the thalamic nuclei for evidence of retrograde degeneration. The cases selected as involving only the striate areas show no thalamic

TABLE V

Average Learning Scores of Animals with Lesions Restricted to the Striate Areas for the Inclosed and Open Mazes Which Were Their First Problems

Subgroup IILa ran the inclosed maze; Subgroup IILb the open. For further explanation, see Table III.

ANIMAL GROUP	NUMBER OF CASES	AVERAGE PERCENTAGE OF LESION	CRITERIA	AVERAGE SCORES	DIFFERENCE	PERCENTAGE	AVERAGE RETARDATION
IILa, Peripherally and cortically operated	3 (18, 100, 103)	11.7	Time	12,007.00	9,669.00	413.56	425.93
			Errors	787.67	688.85	697.08	
			Trials	102.00	63.82	167.16	
IILb, Peripherally and cortically operated	4 (22, 27, 38, 104)	14.8	Time	13,682.00	11,488.00	523.61	711.94
			Errors	1,141.25	1,066.34	1,423.49	
			Trials	99.75	65.20	188.71	

degeneration except in the lateral geniculate nuclei. This indicates that no other primary sensory field than that of visual projection was destroyed. On account of the great importance of such ideal cases for the elucidation of our problem we have treated their learning scores in the same systematic way as we did for the whole subgroup.

Table V presents the average scores of the control cases in Subgroups IILa and IILb for the inclosed and open mazes respectively. In the inclosed maze, the control class of Subgroup IILa is far inferior to the peripherally blinded Subgroup ILa, as judged by all the three criteria of learning. The time, error and trial scores are 12007.00, 787.67 and 102.00 respectively, whereas the corresponding scores of Subgroup ILa are 2047.00, 107.51 and 63.49. The average retardation of the controls is 425.93 per cent, being much higher than that of the entire subgroup, 183.23 per cent. The retardation of the peripherally blinded Subgroup ILa is only 20.88 per cent. The same condition prevails in Subgroup IILb in the open maze. The time, error and trial scores of animals with lesions restricted to the striate areas are 13682.00, 1141.25 and 99.75 respectively, which, with the exception of the last, are much higher than the corresponding scores of the peripherally operated Subgroup ILb, 4705.00, 243.66 and 110.03. The controls show an average retardation based on all criteria of 711.94 per cent, being much higher than the subgroup retardation, 470.09 per cent. The retardation of the peripherally blinded Subgroup ILb is only 186.06 per cent. Thus, the omission of all cases in which there is any reason to suspect invasion of non-visual cortex which might be concerned in maze learning does not reduce the apparent effects of lesions in the striate areas.

From the various controls set forth in the foregoing pages we see that the additional injuries to the subcortical structures and to the non-striate cortical fields do not seriously affect the group scores. In other words, the greater retardation of the cortically operated animals is to be attributed mainly to the destruction of the visual areas.

EFFECTS OF PERIPHERAL AND CORTICAL OPERATIONS UPON RETENTION SCORES

1. *Experimental Data*

In Table VI are given the individual learning and relearning scores for the inclosed and open mazes of animals peripherally blinded and of those blinded before and subjected to cortical operation after training. No arbitrary limit was set to the number of trials for these groups; the animal ran the maze until the criterion of proficiency of ten consecutive errorless trials was attained. Total time spent, total errors made and total trials taken preceding the attainment of this standard in the learning and relearning series are given for each case. When the animals had learned the maze half were set aside for a period of two weeks without training (Subgroups IRa and IRb) and half were subjected to lesions in the striate areas with two weeks' rest following (Subgroups IIRa and IIRb). The groups were then trained to the criterion. We have calculated the absolute savings in the relearning scores for the three criteria and expressed them as the percentages of corresponding learning scores for each case (not given in Table VI). The average of the percentage savings for the three criteria gives the average retention score of each animal for the maze problem, which is to be found in the last column of Table VI.

A word should be said of the savings score. This score is obtained by subtracting the relearning score for a criterion from the corresponding initial learning score. The difference thus obtained indicates the savings in effort on the part of the animal to attain the same degree of proficiency in relearning as in initial learning. That is, it represents what is retained of the maze habit two weeks after completion of learning either with or without the additional operation on the visual areas, as judged by some one of the criteria of learning. The savings score is sometimes negative. In such case it means that the animal required more practice for relearning than for initial learning.

Table VII presents the average scores of learning and relearning

TABLE VI

Learning and Relearning Scores for the Inclosed and Open Mazes of Animals Operated Peripherally and Both Peripherally and Cortically

The percentages of cerebral lesions in the cortically operated cases are presented at the left. Learning and relearning scores for the three criteria, time, errors and trials, are given for each case. Relearning scores of Subgroups IRa and IRb are post-resting scores and those of Subgroups IIRa and IIRb are postoperative scores. "Average retention" is the average of the percentage savings in the relearning scores for the three criteria.

ANIMAL GROUP	NUMBER	SEX	PERCENTAGE OF LESION	LEARNING SCORES			RELEARNING SCORES			AVERAGE RETENTION
				Time	Errors	Trials	Time	Errors	Trials	
For the Inclosed Maze										
				seconds			*seconds*			*per cent*
IRa, Peripherally Operated	3	f		499	29	32	66	3	11	80.69
	6	m		541	35	20	88	3	8	78.39
	21	m		1,273	85	113	0	0	0	100.00
	35	m		1,083	38	16	0	0	0	100.00
	47	f		947	70	37	0	0	0	100.00
	51	f		1,051	50	23	67	2	8	84.95
	67	f		4,544	197	93	63	2	9	95.97
	68	f		4,026	266	97	0	0	0	100.00
	75	f		461	32	37	209	12	30	45.36
	78	m		530	29	28	0	0	0	100.00
	85	f		2,287	137	101	19	1	3	98.49
IIRa, Peripherally and Cortically Operated	14	f	19.4	1,418	91	106	994	99	59	21.82
	15	m	12.5	4,891	107	88	763	38	26	73.11
	23	f		3,130	148	60	(Died)			
	28	f	19.4	668	31	33	1,554	139	112	−240.14
	30	m	10.9	1,563	76	38	0	0	0	100.00
	37	m	13.0	2,707	79	70	3,208	153	17	−12.16
	40	m	17.9	236	21	10	65	5	5	66.22
	42	f	13.7	1,347	115	103	1,494	86	45	23.54
	61	f		1,935	154	62	(Died)			
	63	f	18.5	4,873	160	81	598	45	35	72.13
	77	m	18.1	893	49	28	59	4	1	93.89
	88	m	21.1	1,090	52	58	1,771	65	38	−17.67
	93	f		1,314	87	46	(Died)			
	96	f	10.9	9,947 [8,329]*	521 [453]	259 [150 (61)]	3,153	260	106	59.16
	101	m	9.4	2,948	155	69	5,436	980	264	−299.76

For the Open Maze

IRb, Peripherally Operated	7	m		3,048	150	128	0	0	0	100.00
	20	m		3,436	175	56	133	5	1	97.16
	26	m		1,336	55	21	60	5	1	93.89
	52	m		12,280	550	271	203	5	3	98.78
				[10,257]	[452]	[150 (44)]				
	54	m		7,142	314	253	604	26	35	89.81
				[6,187]	[267]	[150 (58)]				
	71	f		12,260	709	209	(Died)			
				[11,590]	[678]	[150 (36)]				
	72	f		9,074	309	146	0	0	0	100.00
				[9,091]	[309]	[150 (64)]				
	79	m		796	34	9	129	4	17	27.71
	80	f		7,505	416	327	60	3	7	98.78
				[4,893]	[305]	[150 (60)]				
	82	f		2,958	86	27	0	0	0	100.00
	84**	f		1,733	128	108	(827)	(48)	(28)	(62.95)
	92	f		3,292	193	58	99	4	8	93.71
	94	f		8,606	511	228	1,367	69	79	78.66
				[7,252]	[420]	[150 (76)]				
IIRb, Peripherally and Cortically Operated	10	f	18.3	7,034	305	200	1,179	99	63	73.09
				[6,214]	[277]	[150 (69)]				
	16	f	27.5	3,155	192	142	3,421	397	190	−49.67
				[3,223]	[192]	[150 (83)]				
	17	f	13.8	9,417	451	282	14,589	795	457	−64.42
				[6,955]	[342]	[150 (44)]				
	25	f	11.1	2,635	137	137	1,259	63	128	37.60
	29	m	14.0	693	32	18	3,446	236	120	−533.81
	39	f	19.4	5,223	289	218	2,092	261	161	31.93
				[4,160]	[230]	[150 (67)]				

* Scores in brackets are those up to 150 trials in animals which had not learned the maze within that arbitrary limit. These trimmed scores are averaged together with the corresponding scores of the peripherally operated Subgroup ILa (in the inclosed maze) or ILb (in the open maze), of the learning group proper, to give the group average learning scores for the respective maze run as the first problem.

** The animal developed vestibular troubles during the retention period. Its post-resting relearning scores are given, but dropped out from the group average.

TABLE VI—*Concluded*

ANIMAL GROUP	NUMBER	SEX	PERCENTAGE OF LESION	LEARNING SCORES			RELEARNING SCORES			AVERAGE RETENTION
				Time	Errors	Trials	Time	Errors	Trials	
For the Open Maze—*Concluded*										
				seconds			*seconds*			*per cent*
IIRb, Peripherally and Cortically Operated —*Concluded*	57	f	15.7	4,245	227	160	2,507	154	105	35.83
				[4,177]	[224]	[150 (58)]				
	60	f		5,637	176	62	(Died)			
	62	f	15.4	3,594	231	80	901	79	89	43.16
	64	f	16.2	3,337	131	124	4,304	362	79	−56.34
	81	m		2,961	143	132	(Died)			
	87	m		612	23	21	(Died)			
	89†	m		(14,583)	(1,116)	(650)	(Training discontinued)			
				[8,846]	[734]	[150 (32)]				
	97†	f		(28,935)	(2,578)	(650)	(Training discontinued)			
				(16,432)	(1,532)	(150 (4))				
	102	m	8.7	3,323	327	118	1,071	73	91	56.11

† Circumstances forced the interruption of the training of Nos. 89 and 97. The trimmed scores of the former were included in calculating the group averages for the learning of the open maze as first problem, but the scores of the latter were dropped out because of their unduly influences on the group scores.

TABLE VII

Average Learning and Relearning Scores for the Inclosed and Open Mazes of Animals Operated Peripherally and Both Peripherally and Cortically

The averages are based upon all cases in each subgroup which had both learning and relearning scores. The average percentage of cerebral lesions is presented for each cortically operated subgroup. Average time, error and trial scores of learning and relearning are given together with their respective probable errors. Under "Savings" the absolute savings in the relearning scores for the three criteria are presented and under "Percentage" the absolute savings are expressed as the percentages of the corresponding learning scores. The average of the three percentage savings gives the "Average Retention" of the group.

ANIMAL GROUP	NUMBER OF CASES	AVERAGE PERCENTAGE OF LESIONS	CRITERIA	AVERAGE LEARNING SCORES	AVERAGE RELEARNING SCORES	SAVINGS	PERCENTAGE	AVERAGE RETENTION *per cent*
For the Inclosed Maze								
IRa (Peripherally operated	11		Time	1,567.00 ± 280.08	47.00 ± 12.30	1,520.00	97.00	94.36
			Errors	88.00 ± 15.39	2.09 ± 0.89	85.91	97.63	
			Trials	54.27 ± 7.34	6.27 ± 1.29	48.00	88.45	
IIRa (Peripherally and cortically operated)	12	15.4	Time	2,715.00 ± 512.49	1,591.00 ± 303.71	1,124.00	41.40	12.57
			Errors	121.42 ± 24.89	156.17 ± 50.43	−34.75	−28.62	
			Trials	78.58 ± 12.01	59.00 ± 13.88	19.58	24.92	
For the Open Maze								
IRb (Peripherally operated)	11		Time	5,407.00 ± 714.47	241.00 ± 79.56	5,166.00	95.54	93.77
			Errors	253.91 ± 34.84	11.00 ± 3.98	242.91	95.67	
			Trials	138.55 ± 22.14	13.73 ± 4.67	124.82	90.09	
IIRb (Peripherally and cortically operated)	10	16.0	Time	4,266.00 ± 495.62	3,477.00 ± 825.70	789.00	18.50	3.25
			Errors	232.20 ± 24.00	251.90 ± 45.73	−19.70	−8.48	
			Trials	147.90 ± 14.92	148.30 ± 23.30	−0.40	−0.27	

for the mazes of animal groups blind from birth and those blind before and cortically operated after initial learning. Only cases with complete relearning scores were included in the calculation of the group scores. The average time, error and trial scores of learning and relearning are presented with their corresponding probable errors. The absolute savings in the average relearning scores were calculated and expressed as the percentages of the corresponding average learning scores. The average of the percentage savings for the three criteria represents the average retention score of the subgroup for the maze problem.

In view of the great individual differences in the retention of maze habits, we have also determined the group median of the individual average retention scores (Table VI) for the retention groups. As we shall see presently, the group medians are in close harmony with the group averages.

2. Effects of Peripheral Blinding on the Retention of the Maze Habit

We will consider first the influences of peripheral operation on the retention scores after an interval of two weeks without training. Table VII presents the average learning and relearning scores of the blind animals. The maze problems will be treated separately.

a. Inclosed Maze. The peripherally blinded Subgroup IRa relearned the inclosed maze very readily at the close of the retention period. The group percentage savings for time, errors and trials are 97.00, 97.63 and 88.45 respectively, which, when averaged together, gives the group an average retention of 94.36 per cent. A still higher retention is attested by the median of individual retention scores (Table VI), which is 98.49 per cent, being perhaps more representative of the real situation. Five of the eleven animals, or 45.45 per cent, showed perfect retention. Unfortunately, we have no normal retention score for this maze to compare with the peripherally blinded, but in all probability the normals can hardly be better than the latter. Thus, animals lacking vision from infancy retain the maze habit practically unimpaired for a period of two weeks and the absence of vision does not seem to affect retentiveness.

b. Open Maze. To what extent does peripheral blinding influence the retention of the open maze habit in which vision plays a much greater rôle? We have demonstrated that the blind animals are seriously handicapped in learning the open maze. Once the habit is formed, however, it is well retained. Indeed, the blind Subgroup ILb relearned the open maze after two weeks of no training just as promptly as the same type of animals relearned the inclosed maze for which vision is not essential. The group percentage savings for time, errors and trials are 95.54, 95.67 and 90.09 respectively, with a group retention score of 93.77 per cent. The median of the individual retention scores (Table VI) runs as high as 97.16 per cent, again very close to that for the inclosed maze. Three out of eleven animals, or 27.22 per cent, made perfect retention record. In short, the effect of absence of vision on the retention of the open maze habit is certainly very slight.

We are now in a position to test the functions of the visual areas in the maze learning of the blind rats. We have shown that such animals can retain the maze habit unimpaired for two weeks. They have certainly not learned the maze in terms of visual cues or of any acquired visual space system. If then the destruction of the striate cortex after training in such animals should produce a loss of the maze habit, this would be evidence that the visual projection area has participated in learning by the performance of some non-visual function.

3. *Effects of Cortical Operation on the Retention of the Maze Habit*

Upon the completion of learning, animals in Subgroups IIRa and IIRb were deprived of the visual areas. At the end of fourteen days they were tested for retention.

a. Inclosed Maze. Subgroup IIRa first learned the inclosed maze with promptness characteristic of blind animals in this maze. They lost on the average 15.4 per cent of cortical tissues following the destruction of the visual areas. The percentage savings for time, errors and trials are 41.40, −28.62 and 24.92 respectively, being far below the corresponding scores of the peripherally blinded, which are more than 90 per cent (Table VII). We compare with the controls their retention scores for errors.

SUBGROUP	PROBLEM	RETENTION SCORE FOR ERRORS	DIFFERENCE IN SAVINGS
IRa (Peripherally operated)	Inclosed maze	97.63	
IIRa (Peripherally and cortically operated)	Inclosed maze	−28.62	126.25

The postoperative retention is worse than *nil*, as judged by this most reliable criterion. The average retention score, based on all criteria, of the subgroup is 12.57 per cent, which is only one eighth that of the peripherally blinded Subgroup IRa (94.36 per cent). The median of the individual retention scores is higher, 41.35 per cent, still far below that of the merely blind animals (98.49 per cent).

b. Open Maze. Subgroup IIRb with an average lesion of 16.0 per cent retained almost nothing of the open maze habit after the operation. Both the error and trial scores are worse than those of initial learning. The percentage savings for time, errors and trials are 18.50, −8.48 and −0.27 respectively, while the corresponding figures for the peripherally blinded are all above 90 per cent (Table VII). We again reproduce the retention scores for errors for comparison:

SUBGROUP	PROBLEM	RETENTION SCORE FOR ERRORS	DIFFERENCE IN SAVINGS
IRb (Peripherally operated)	Open maze	95.67	
IIRb (Peripherally and cortically operated)	Open maze	−8.48	104.15

No trace of the open maze habit is demonstrable after the removal of the visual areas, as judged by the error criterion. The group shows an average savings score of 3.25 per cent, which is one thirty-first that of the peripherally blinded Subgroup IRb (93.77 per cent). The group median retention is 33.88 per cent, much higher than the average retention, but it is significantly lower than the corresponding median of the blind animals (97.16 per cent).

Thus, for both the open and the inclosed mazes the results are the same. When animals blind from birth have learned the mazes, destruction of the cerebral visual areas produces an almost complete loss of the habit. The visual projection areas, although deprived from birth of any primary visual function, play a dominant rôle in the performance of the maze habit.

4. *Summary of Data on Retention*

The horizontal bars in Figure 2 show graphically the postoperative loss of the maze habit due to cortical lesions. The length of the bars is proportional to the amount of retention (percentage savings in retraining) of the maze habit by the differently operated groups. The continuous lines represent group average retention; the broken lines, the group median retention. From the histogram we see that the median scores are invariably higher than the average scores. But the loss following cortical lesion in comparison with the control group is striking, no matter whether the average or median is used as criterion of judgment.

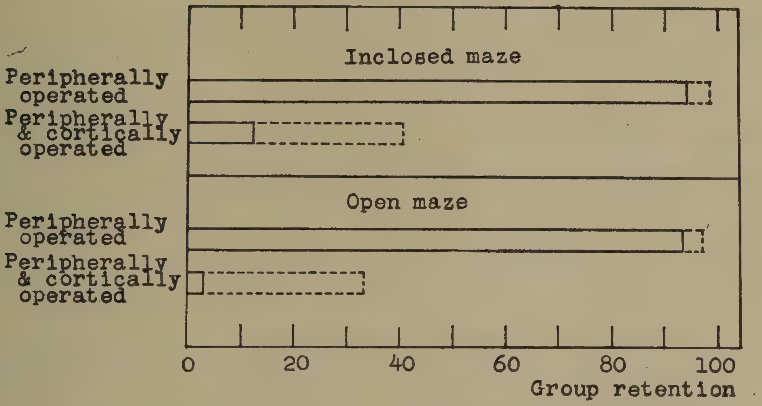

FIG. 2. HISTOGRAM OF THE AVERAGE AND MEDIAN RETENTIONS OF THE MAZE HABITS BY THE DIFFERENTLY OPERATED ANIMAL GROUPS
——— group average; ---------- group median

We sum up in a few lines the outstanding points of our data on retention. After a resting period of fourteen days the retention of the maze habits by the blind animals is almost perfect. A fair proportion of such animals actually show perfect retention. The destruction of the visual areas upon completion of learning by such blind animals erases almost all has been learned. In relearning the maze, they are hardly better than before they had any experience in it. The visual cortex thus has some important function in the maze habit although the animals have had no opportunity for the formation of any visual habits.

5. Possible Influences of Additional Subcortical and Non-striate Cortical Injuries on Retention Scores

It is essential to control our results as to the possible effects of additional subcortical and non-striate cortical lesions, for such minor wounds might somehow be responsible for the post-operative loss of the habit. In instituting the controls we shall follow the same lines as in dealing with the scores of the learning groups.

a. Possible Influences of Subcortical Injuries. Table VIII presents a comparison of the retention scores for errors of animals with and without subcortical lesions, in addition to the destruction of the visual areas, for the two maze problems. We first take up Subgroup IIRa in the inclosed maze. Fortunately, we have no cases with thalamic, mesencephalic or extensive hippocampal injuries. There are six cases with light hippocampal lesions, but they made a better record than those free from such involvements. Their retention scores for errors are −9.31 and −37.59 per cent respectively, both being far inferior to that of the blind animals (97.63 per cent).

On the other hand, the records of Subgroup IIRb in the open maze present a somewhat different situation (Table VIII). The additional injuries to the thalamic, mesencephalic and hippocampal structures apparently reduced the retention of the maze habits. But the difference between animals with and without such involvements is relatively small. All classes of animals with subcortical injuries do not show any retention of the habit, and the retention of those without such involvements centers around zero. There are too few cases in the thalamic and mesencephalic classes to claim much importance. Any of the six retention scores for errors, −176.34 vs. 1.55; −48.33 vs. 0.32; and

TABLE VIII

Comparison of the Retention Scores for Errors of Animals with and without Subcortical Lesions in Addition to the Removal of Visual Areas for the Inclosed and Open Mazes

Under "Effect" the apparently positive (+) or negative (−) influence of the additional subcortical lesions upon the retention score is indicated.

ANIMAL GROUP	KIND OF LESION	WITH SUBCORTICAL LESION						WITHOUT SUBCORTICAL LESION					EFFECT
		Cases (experimental numbers)	Number of cases	Average percentage lesion	Average error score of learning	Average error score of relearning	Retention score for errors	Number of cases	Average percentage lesion	Average error score of learning	Average error score of relearning	Retention score for errors	
							per cent					*per cent*	
IIRa, Inclosed Maze	Thalamic	No such case											
	Mesencephalic	No such case											
	Hippocampal:							6					
	Light	14, 28, 37, 63, 77, 88	6	18.3	77.00	84.17	−9.31	(15, 30, 40, 42, 96, 101)	12.6	165.83	228.17	−37.59	−
	Extensive	No such case											
IIRb, Open Maze	Thalamic	64	1	16.2	131.00	362.00	−176.34	9	16.0	243.44	239.67	1.55	+
	Mesencephalic	39, 64	2	17.8	210.00	311.50	−48.33	8	15.6	237.75	237.00	0.32	+
	Hippocampal:							4					
	Light	10, 29, 39, 57	4	16.9	213.25	187.50	12.08	(17, 25, 62, 102)	12.3	286.50	252.50	11.87	+
	Extensive	16, 64	2	21.9	161.50	379.50	−134.98						

−61.45 (average of two) vs. 11.87, may be substituted for the subgroup score, −8.48 per cent, without altering the inferiority of the cortically operated to the blind animals whose corresponding score amounts to 95.67 per cent. Thus, an additional minor injury to the subcortical structures seems not to exert any substantial influence on the group retention scores. The postoperative loss is not due primarily to any subcortical lesions.

TABLE IX

Average Learning and Relearning Scores for the Inclosed and Open Mazes of Animals with Lesions Restricted to the Striate Areas

Subgroup IIRa ran the inclosed maze; Subgroup IIRb, the open

For further explanation, see Table VII

ANIMAL GROUP	NUMBER OF CASES	AVERAGE PERCENTAGE OF LESION	CRITERIA	AVERAGE LEARNING SCORES	AVERAGE RELEARNING SCORES	SAVINGS	PERCENTAGE	AVERAGE RETENTION
								per cent
IIRa, Peripherally and cortically operated	5 (15, 30, 42, 96, 101)	11.5	Time	4,139.00	2,169.00	1,970.00	47.60	9.46
			Errors	194.80	272.80	−78.00	−40.04	
			Trials	111.40	88.20	23.20	20.83	
IIRb, Peripherally and cortically operated	3 (17, 25, 102)	11.2	Time	5,125.00	5,640.00	−515.00	−10.05	−12.56
			Errors	305.00	310.33	−5.33	−1.75	
			Trials	179.00	225.33	−46.33	−25.88	

b. Possible Influences of Non-striate Cortical Lesions. We have calculated the average learning and relearning scores for time, errors and trials for the control cases in Subgroups IIRa and IIRb with lesions approximately restricted to the striate areas (Table IX). The non-visual nuclei of the thalamus were examined and no trace of degeneration was found in their cellular elements. It is thus assured that no primary sensory field was involved except that of visual projection. In Nos. 17 and 25 in Subgroup IIRb, the lesions extended farther beyond the strictly striate areas than in other cases. Subgroup IIRa in the inclosed maze shows percentage savings in the relearning scores for time, errors and trials of 47.60, −40.04 and 20.83 respectively, which are far less than the corresponding scores of the peripherally blinded Subgroup IRa, 97.00, 97.63 and 88.45 respectively. The average retention of the control cases is 9.46 per cent, being close to the subgroup score, 12.57 per cent. Both constants are much lower than that of the blind animals, 94.36 per cent.

The control cases in Subgroup IIRb in the open maze show no retention as judged by any of the three criteria. The percentage savings in the relearning scores for time, errors and trials are −10.05, −1.75 and −25.88 respectively, in striking contrast to the high scores of the peripherally blinded Subgroup IRb, 95.54, 95.67 and 90.09 respectively. The average retention of the control cases is −12.56 per cent, which is even worse than the subgroup score, 3.25 per cent. Both are inferior to the blind animals whose average retention runs as high as 93.77 per cent. Thus, the inclusion of cases with additional non-striate cortical lesions in the whole series does not alter seriously the results from those obtained with cases in which the lesions are restricted to the striate areas.

From the various controls instituted in the foregoing pages it seems safe to say that the inclusion of cases with some minor additional subcortical and non-striate cortical injuries in computing the group constants does not affect the latter in any particular direction. In short, the strikingly poor postoperative retention of the maze habits by the cortically operated is to be attributed mainly to the removal of the visual areas.

INTERPRETATION

We come finally to interpret the experimental results set forth in the preceding pages. Destruction of visual areas of animals blind from birth results in greater retardation in the learning and postoperative relearning of the maze than does enucleation of eyes alone. Since the visual areas have been put out of visual function by the peripheral blinding in infancy, the deterioration following the removal of these areas can only be due to the loss of something other than visual function. In other words, the visual areas have some non-visual function which normally participates in maze learning and whose elimination induces serious retardation.

Other interpretations are still, however, possible. In his criticism of Lashley's results pertaining to the relation between the extent of cortical lesion and degree of retardation, Hunter ('30, '31) stresses the sensory loss, i.e. the involvement of other sensory areas than the one in question. This criticism may be directed to the present study. It is true that in many of our cortically operated animals the lesion extended out of the strictly visual cortex, i.e. the striate area. But we have shown that the deterioration is just as pronounced in cases where the lesion is limited to the striate areas and that the invasion of other sensory projection areas is too slight to account in itself for the defects of learning or postoperative loss of the habits. In all the experiments the major effects must be ascribed to the lesion in the primary visual areas and there is no justification for the assumption that direct damage to any other areas has influenced our results significantly.

We have elsewhere discussed the significance of diffuse circulatory and nutritive changes in experiments of this type. (Tsang, '36.) Both the anatomical and experimental evidence oppose the assumption of such agencies. We have shown that widespread circulatory changes do not follow lesions to the rat's cortex but that, on the contrary, circulatory and, presumably, nutritive conditions are normal up to the boundaries of the lesion. Lashley ('29, '35), Bard and Brooks ('34) have shown normal functioning of small residual portions of specialized fields.

These considerations force the conclusion that the disturbance of maze learning and retention found in our experiments is due to the destruction of the visual areas, the primary visual projection centers, and not to any direct effect of the incidental injury to other cortical structures.

On a theory of sensory functions of the visual areas, the maze efficiency of animals blind from birth should be the same either with or without these areas. But, as a matter of fact, the additional operation on these areas produces a much greater deterioration in the learning and retention of the maze than does peripheral blinding alone. This evidently means that the striate areas of such blind animals actually function in maze learning. Since these areas have never been excited by spatially determined impulses from the eyes, their function can not be visual in any accepted meaning of the term—sensory, perceptual or neumonic.

The exact nature of this non-visual function of the visual cortex remains to be revealed. There seems to be two alternative possibilities:

a. The visual cortex might serve to organize non-visual excitations in some sort of perceptual framework constituting an instinctive or innate spatial system which might be primary for all space perception. Some of the Gestalt material vaguely suggests this sort of thing. The perception of "thing" in space-figure ground relations and the like seems independent of the sensory mechanism and might depend upon a non-sensory space-organization in the cortex. There is no direct evidence for this. Recently Lashley and Russell ('34) demonstrated the probably innate character of the perception of spatial depth in the visual field in the rat, but their findings are not relevent to the point in question, for at most they only show that when vision is present it is organized in certain ways. Moreover, Gelb and Goldstein ('20) have shown in one of their studies that patients with visual space perception disturbed retain normal kinesthetic space perception. In other words, the existence of innate space-framework in the cortex lacks factual support.

b. The only alternative .left is some non-specific facilitative process. The visual cortex is indispensable for the smooth-running of the cerebral integrating mechanism, contributing to the functional efficiency of other parts of the brain, which, in all probability, also have such functions in common. Though out of visual function after enucleation of eyes in infancy, the visual areas remain integral parts of the brain and facilitate central integration with their non-visual function. The cerebral mechanism is thus maintained at a high level of efficiency and a good maze performance is the result. On the other hand, with the destruction of the visual areas, the remaining parts suffer in efficiency. Something is lost, which normally helps keep the integrating mechanism a smooth-going concern. The cortically operated animal is poorly integrated in its activities and betrays symptoms nothing short of dementia.

The difference in the maze behavior of animals merely blind from birth and those with the additional destruction of the visual areas reflects the difference in the working conditions of the brain. The blind animals exhibited no behavior peculiarities which degraded the quality of their maze running. On the other hand, blind animals when deprived the visual areas displayed all the behavior peculiarities which we listed elsewhere (Part I, pp. 40–41). Most typical of all was the running of a straight course, usually the first three sections, back and forth, until errors were accumulated to one hundred or more. Without the contribution of the non-visual visual cortex the animal ceases to be what it normally is. It is more or less disintegrated and demented, so that it is incompetent to run a maze, a job so easy for the blind animal.

Thus, the visual area seems to have two widely diverse functions. It is the most specialized of all sensory areas of the cerebral cortex. The visual projection field is spatially localized; a definite correspondence between retinal quadrants and parts of the striate area has been demonstrated in the rat (Lashley, '34) and this structural differentiation is intimately bound up with detail vision. However, apart from the highly specific visual functions, it also exercises some general, perhaps facilitative, influence upon all other parts. In turn, it is perhaps also facilitated in the execution of its functions by a similar influence from other parts. This is essentially the view of Lashley who says: "In more complex functions, such as learning and retention of the maze habit, the visual area seems essential yet non-specific, contributing facilitation to the total neural organization yet essentially equivalent to other cortical areas. The same area may at times function as a highly differentiated system, at others as a unitary mass" ('31b).

Flourens ('42) declared the mutual facilitation of brain parts as a general rule, "Qu'indépendamment de l'*action propre* de chaque partie, chaque partie a une *action commune* sur toutes les autres, comme toutes les autres sur elle." It is probable that the presence of such a general function common to all parts of the brain makes possible the unitary functioning of the brain as a whole.

GENERAL SUMMARY

One hundred and one rats were blinded in infancy by enucleation of eyes to eliminate the primary visual function of the visual cortex. They were trained at about three months of age in the inclosed alley maze and the open skeleton maze of same pattern. The blind animals were divided into two groups, one for tests of initial learning and the other for tests of postoperative retention of the maze habits. The effect of additional destruction of the visual areas in the blind animals on initial learning was compared with that of peripheral blinding alone. The retention of the maze habit following the cortical operation was compared with that after two weeks' rest. The main points of our results are as follows:

1. Peripheral privation of vision has little retarding effect on the formation of the inclosed maze habit, but it exerts a marked retardation on the learning of the open maze.
2. Additional destruction of the visual areas in the blind animals is by far more detrimental than peripheral blinding alone. This is true for both the inclosed and the open mazes.
3. Peripherally blinded animals retain the maze habit, inclosed or open, almost perfectly after a resting period of two weeks.
4. Removal of visual areas after the formation of a maze habit annihilates virtually all has been learned. This is true for both maze habits. The visual areas of the blind animals actually participate in maze learning.
5. Controls show that the deterioration is really due to the lesions in the striate areas.
6. The maze behavior of animals blind from birth compares favorably with that of the normals, but the quality of maze performance of animals with the additional operation on the visual areas is decidedly poor, betraying symptoms of central disintegration or dementia.
7. Since the visual areas are out of visual function from birth,

the greater deterioration following their removal, in comparison with that after peripheral blinding, can only be due to the loss of the non-visual, general and probably facilitative functions with which they normally contribute to the general integrative action of the brain as a whole.

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PLATES I AND II

Diagrams of the Extent and Locus of the Lesions in the Cortically Operated Animals

Only dorsal views of the lesions are given. The lateral views of a few extensive lesions have been reconstructed for measurement but not reproduced. The figure at the left is the identification number of the case used in the text and the tables; that at the right, the percentage of the cortex removed.

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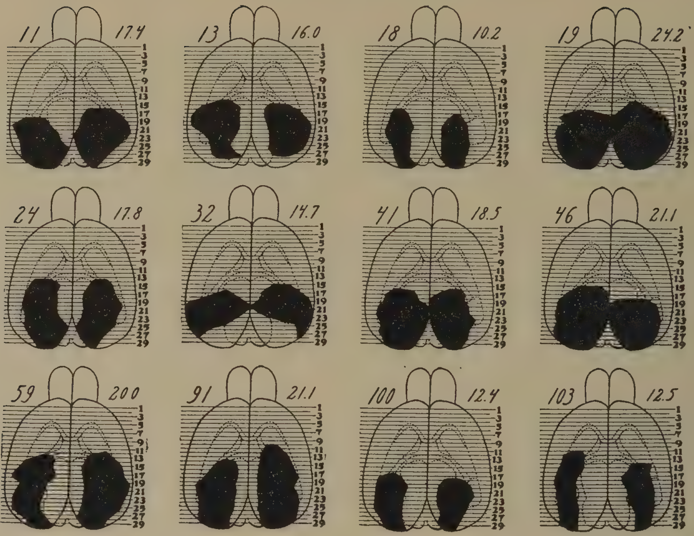

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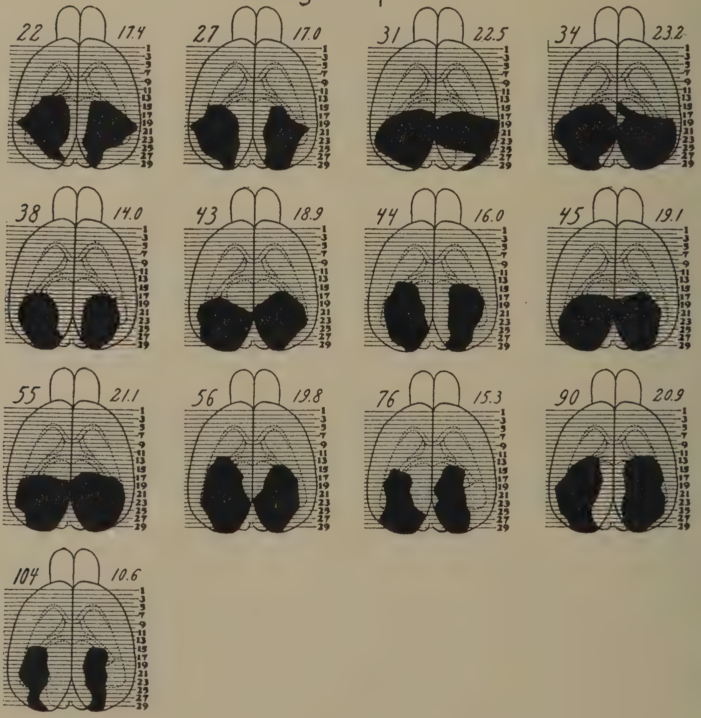

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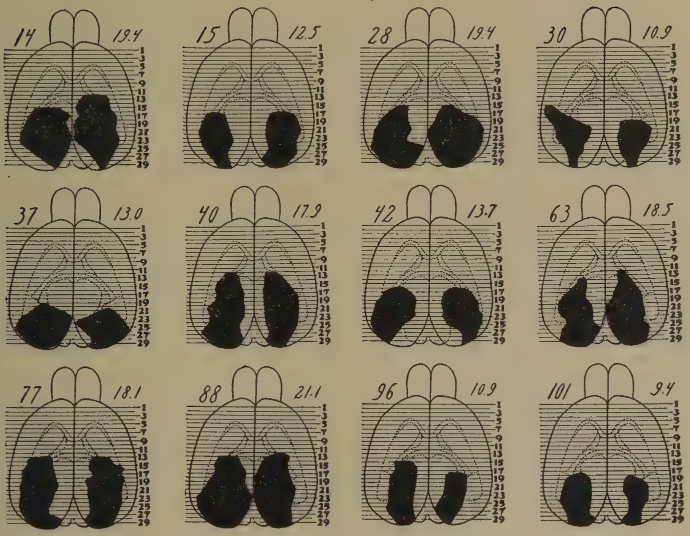

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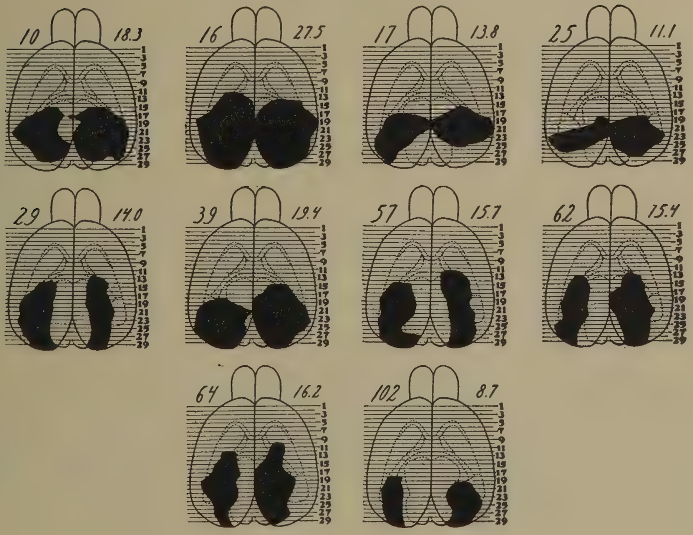

PLATE II

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Vol. 12 No. 3 JANUARY, 1936 Serial No. 58

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THE AVIAN VISUAL SYSTEM

I. CEREBRAL FUNCTION OF THE DOMESTIC FOWL IN PATTERN VISION

BY
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THE AVIAN VISUAL SYSTEM

I. CEREBRAL FUNCTION OF THE DOMESTIC FOWL IN PATTERN VISION[1]

JOHN D. LAYMAN

University of California at Los Angeles

I. INTRODUCTION

a. Avian vision compared to vision in other forms

The relative importance of vision and other senses in determining the behavior of different species of animals presents some interesting problems, both from the standpoint of evolution and from that of nervous organization. In some lower vertebrates as fish (Schaller, 1926) and reptiles (Casteel, 1911), detail vision seems well developed. It plays an important rôle in the life economy of these animals and is readily demonstrated under controlled experimental conditions. In birds, the primacy of vision is especially prominent. The apparent helplessness of most birds at night along with their dependence upon vision for feeding and for dexterously guiding them in their rapid flights bear witness to this fact.

In the macrosmic mammals, vision undergoes regression. Many of these are little handicapped when deprived of their eyes and in their normal activities they seem to make little use of vision (Tsang, 1934). In the rat (Lashley, 1912; Munn, 1929) and dog (Johnson, 1916c; Szymanski, 1918) it has been difficult to demonstrate even crude detail vision under controlled conditions. When a method is devised to force these animals to visual attention, they prove to have relatively good pattern vision

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[1] The writer wishes to acknowledge his appreciation to Dr. K. S. Lashley for assistance in this project.

Submitted to the faculty of the University of Chicago in partial fulfillment for the doctorate degree.

(Lashley, 1930; Rizzolo, 1932), yet under ordinary conditions of life they seem dominated by other sense modes. It is only in the primates that vision acquires a predominance among the senses comparable to that in birds.

The reason for this dominance or suppression of vision in the higher vertebrates is not obvious from the structure of their eyes, nor from that of their central nervous system, but is to be sought in the physiological organization of the central visual pathways.

Besides throwing light on the problem of visual dominance, analysis of the visual function in birds offers a means of attack upon problems of binocular fusion. One of the most important cues to the perception of depth rests upon the fact of the binocular disparity existing between the two eyes in the perception of an object. In birds there is an arrangement in various species which fluctuates in some, from perhaps a complete overlapping of the visual fields, as in owls, to perhaps a complete separation in others, as in chickens. In some species there is no fovea; others have one and still others have two with various positions in the eye. There is complete decussation of the fibers in the optic nerve. Nevertheless, the rapid flight and accurate visual reaction to distance indicates a high degree of binocular integration carried out by a quite different structural organization from that of mammals.

b. Neural correlates of vision in birds and mammals

Anatomically the known nervous correlates of vision in birds and mammals differ tremendously. The point for clear detail vision is definitely known to be the fovea in primates. Yet according to Slonaker (1921) the domestic hen possesses no fovea, while on the other hand most birds possess one, and some two (Slonaker, 1897; Wood, 1917). In this later case the second or peripheral fovea is used in binocular vision.

In mammals, the fibers from the retina partially decussate in the optic chiasma, whereas in birds there is a complete crossing (Perlia, 1889). Further centrally in birds Perlia found a division into a medial and a lateral optic tract. These he correlated with

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the nucleus of the medial optic root and the optic lobes respectively.

The central mechanism for detail vision in mammals is found in the occipital cortex. In primates and rodents, where the anatomic projection has been studied carefully, there is an accurate projection of the retina upon the surface of the cerebral cortex. Birds however, do not possess a highly developed cortex for a retinal projection although for them vision is one of the most important, if not the most important sense. Accordingly we see that there is great confusion as to the relation between visual dominance in these various animals and the central neural correlates. The question naturally arises concerning the nature of the central structure which accounts for the high development of vision in birds. Is the primitive cortex of the bird of primary importance for vision, or has evolution turned in another direction from the mammalian system and given increased powers to the optic lobes, hyperstriatum, or other striatal mass.

II. ANATOMICAL CONSIDERATIONS

a. Cortex

When the term cerebral cortex is used in avian literature, confusion at once arises. In mammals with a six layered cortex, the problem is simple. In birds however, even the best authorities differ as to what is designated by the word. Craigie (1929a) has a good summary of the diverging opinions on this point. Bumm in 1883, and Edinger, Wallenberg and Holmes in 1903 believed the whole striatum to be covered with cortex, while Kalischer in 1905 believed cortex was found only in the "wulst" region. (This "wulst" region in the chicken is a dorso-medial swelling in the anterior half of the hemispheres.) Later, Rose (1914) included only the area praepyriformis and septum pellucidum as cortical. Huber and Crosby (1929) recognize a hippocampal formation, entorrhinal and paraentorrhinal areas, and a dorsolateral surface area, as cortical. Of this latter striatal covering, they state that its inclusion as an area of cortex or not depends upon the definition of cortex. Craigie (1929b) dealing with the Australian Kiwi, finds cortex over most of the dorsal and lateral striatum and in the ventral praepyriform area.

b. Striatum

Since many excellent descriptions of the avian striatal masses have been given in minute detail, only the major forebrain cell masses will be reviewed here. The recent excellent article by Huber and Crosby (1929) has been followed in terminology.

Figure 1 shows various levels of the bird forebrain. The letters indicate areas and correspond to the letters used by Rose in 1914 but the significance of these letters has been converted into the terminology of Huber and Crosby. The six different levels are indicated on the surface diagram of figure 2.

At the anterior pole, the whole forebrain with the exception of the basal olfactory nuclei is accessory hyperstriatum (*B*). At the level of the middle of the olfactory bulb two other large nuclei appear on the ventral surface and push the accessory hyperstriatum dorsally as seen in section 1 of figure 1. Traced farther posteriorly in sections 2, 3 and 4 the hyperstriatum accessorium is seen to diminish in size dorso-ventrally until, just before the anterior commissure it vanishes.

The first to appear of the two large ventral nuclei mentioned above is the hyperstriatum (*D*). This spreads out as seen in section 1 of figure 1 and is pushed upwards from its ventral position by the neostriatum. It fans out as in sections 2 and 3 and makes a gradual transition from this condition in the anterior region to that seen in sections 4 and 5 where it is pushed to the midline and eliminated.

The neostriatum (*G*) is the second of the two large basal nuclei previously mentioned, which take origin in the region of the olfactory bulbs. It continues posteriorly to the tip of the occipital pole as the largest mass of the forebrain (see sections 1 to 6, figure 1).

In sections 2, 3, 4 and 5 the neostriatum itself is seen to be pushed dorsally by four other nuclear masses of the forebrain. The first of these masses, the nucleus basalis (*R*) is seen only in the anterior regions (section 2). The second is the paleostriatum

(*H*) (sections 2 to 5) which appears just a few sections behind the nucleus basalis and continues posteriorly becoming smaller after the anterior commissure is reached and vanishing just caudal to the end of the hyperstriatum. A group of large cells (Sections 3 and 4) are found in the paleostriatum and called by Huber and Crosby paleostriatum primitivum (*J*). The other two masses are the ektostriatum (*S*) found in front of the anterior commissure (section 3) and the archistriatum (*K*, section 5) found posterior to the anterior commissure. The basic thalamic and midbrain masses are best seen in sections 4, 5 and 6.

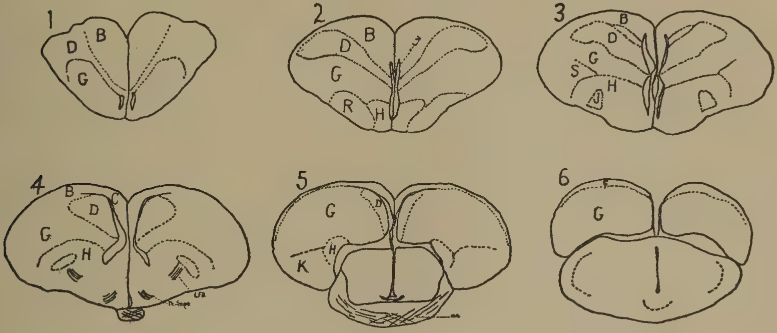

Fig. 1. Cross Sections of the Chicken Forebrain
For significance of lettering see text

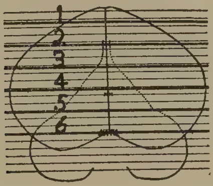

Fig. 2. Dorsal View of the Chicken Forebrain Showing the Levels of the Six Cross Sections of Figure 1

The homologues for all these structures with mammalian forms are not known. Paleostriatum is generally conceded to be homologous to the globus pallidus; the hyperstriatum inferius perhaps corresponds to the caudate and putamen; and the archistriatum is believed to be homologous to the nucleus amygdala of mammals.

Numerous fiber bundles pass out through the paleostriatum into the forebrain, but in a consideration of cortex only two bundles are of importance. The tractus septo-mesencephalicus connects the septum and adjacent cortex with the thalamus; and tractus thalamo-frontalis connects the thalamus with the anterior cortical areas.

III. HISTORICAL REVIEW

a. Vision in normal chickens

Many experiments on normal chickens have been performed showing the character of vision in these birds. Katz and Revesz (1909) by gluing rice to the floor and mixing with it loose wheat, trained chickens to avoid the rice and choose the wheat. They even trained the chicks to discriminate between triangles, circles, and squares that were cut out of peas. Doubt of course exists as to the value of an experiment employing a method such as that used by Katz and Revesz. However the experiments of Breed (1912), Bingham (1913, 1922) and Munn (1931) proved quite conclusively that chickens can discriminate between circles, squares, and triangles. These experimenters equated their figures both as to brightness values and size. Johnson in 1914, made a different attack on the question of avian vision. He determined the stimulus threshold for visible striae in chickens and found that these birds could make accurate discriminations even when the striae subtended an angle of 4 minutes 9 seconds. Two years later (1916a) this same experimenter showed that the ability of the common fowl to discriminate between different widths of striae was lost when the difference in width was reduced to a value between 33 and 40 per cent of the wider stripe. He further determined (1916b) that chickens could accurately discriminate between vertical and horizontal lines, but the threshold of discrimination was reached when the vertical-horizontal relationship was reduced to an angle of 25 to 40 degrees.

b. Electrical excitability of the avian forebrain

The divergence of opinion concerning the avian cortex is paralleled by contradictory evidence on the electrical excitability of the bird brain. David Ferrier (1886) found a spot in the pigeon brain (medial and just behind the center of the brain in a rostrocaudal direction) that provoked an "intense contraction of the opposite pupil" when electrically stimulated. Boyce and Warrington (1898) also working on the pigeon, obtained the same response to faradic stimulation in a larger and more median area. In 1900, Kalischer localized by electric stimulation, areas for closure of the eyes and movements of the extremities, jaws, and limbs. Rogers (1922a), with perhaps an improved technique, obtained several points on the surface of the pigeon brain excitable to electric stimulation. Approximately the same area as that determined by Ferrier produced contraction of the opposite eye, while bilateral winking was produced by an area just lateral to the above named region. Contradictory evidence to the above has been obtained in the work of Popa and Popa (1933). These workers could obtain no response from the cerebral cortex with any intensity of either mechanical or electrical stimulation, even by plunging the electrodes deep into the hemispheres. They did find, however, localization of all motor activities in the midbrain. Like Rogers, they used pigeons. (In the chicken brain by using faradic stimulation, I have localized a motor area for contraction of the pupil of the opposite eye, corresponding approximately in location to the area indicated by Ferrier and Rogers for the pigeon.)

c. *Extirpation work on the bird forebrain*

In the literature of the past describing the anatomy of the bird forebrain, or reporting experiments performed thereon, two principle faults appear. In the first place, there has been no consistency in nomenclature of structures. Moreover, some workers have applied terms to one structure which have been used by other workers to indicate different structures. Secondly, where cerebral ablations have been performed, it has not been the general rule to report necropsies.

Quite uniformly, experimenters have reported that cerebral ablations in birds produce visual disturbances. Their operations have been performed on all parts of the forebrain and as a result, all parts of this mass have been looked upon as producing visual anomalies. Whether the defect in the various cases resulted from the brain injury in a specific region, or resulted because of a lowered mentality of the experimental subjects is not considered.

Extirpation procedures in birds have been performed for over a century. Rolando in 1823, by using a spatula removed cerebral tissue in the parietal region and produced inaccuracy in seizing grain. In 1842, Flourens produced unilateral and bilateral cerebral ablations in pigeons and hens. In the former type of destructions he reported blindness in the opposite eye whereas total blindness resulted from bilateral decerebration. On the other hand, Longet (1842) removed both hemispheres in pigeons and stated that these animals still flew. Whether they could see or whether they struck obstacles is not mentioned. Schrader's work in 1889 on decerebrate birds showed visual deficiencies which were confirmed by Boyce and Warrington in 1898. The latter found that interference with one hemisphere produced a "deficiency of vision in the opposite eye," and that "This result occurs after removal of the anterior or posterior portion of the cerebral hemisphere." Edinger (1895), from anatomical considerations, believed that the occipital pole was visual, and Kalischer (1900) from experimental work, arrived at the same conclusion. Treves and Aggozzatti (1901) worked on bilaterally decerebrated pigeons. They reported that one bird learned to fly back to its perch from new positions in the room, thus indicating that it could still see. In 1918, Martin and Rich working on white leghorn chickens found that with just the upper pallial layers destroyed, feeding was normal, indicating that vision was still intact. Shaklee (1921), moved by the work of Martin and Rich began to work on decerebrate pigeons. Although this experimenter made no visual tests, the results indicate the absence of vision. A great amount of work on decerebrate pigeons has been done by Rogers (1922b). When he obtained unilateral decerebration (checked by histological work) he, like many others, obtained visual defects in the opposite eye. In quite recent years, Gemelli and Pastori (1930) after first training chickens to discriminate colors, decorticated them bilaterally. They found that the animals could be retrained to discriminate colors, showing that this form of vision was still functional. Moreover the fact that these animals discriminated various grains, points to the retention of a crude detail vision. Although many other workers have performed extirpation experiments on birds, their results do not indicate the presence or absence of vision after the lesions had been made.

A brief résumé of previous work thus indicates that with one exception, experimenters have been able to obtain motor responses by electrical stimulation of the forebrain; but agreement as to the locus of stimulable areas and results obtained, is by no means perfect. Other experimenters by using extirpation methods quite unanimously find visual disturbances resulting from cerebral ablations. The tests for vision in these cases however have all been crude and the failure on the part of the animal to react to visual stimuli cannot be taken as proof of blindness.

IV. PROGRAM OF STUDY

a. Statement of problem

Before we can attack such problems as those of ocular dominance or binocular fusion, for which the study of birds promises to be of especial value, we must determine the rôle of the various optic structures in detail vision. We have therefore undertaken an analysis of the effects of destruction of various central nervous structures upon the chicken's ability to differentiate visual patterns. The present study is concerned with the cerebral hemispheres, and principally with the cortex. The experiment was outlined to answer the following questions.

1. Is there an area of the cortex of the chicken essential for pattern vision, such as Lashley (1931) has found to be the case in the rat?
2. If there is no specific visual cortical area, what part if any, does the cortex play in vision?
3. Is any area of the striatal mass more influential in vision than the rest of the mass?

The previous discussion of avian cortex means that in any attempt to destroy this pallial covering we would of necessity either (*a*) limit the lesions to agree with one anatomist's conception of what is cortex, (*b*) attempt to destroy all areas recognized by all writers. The latter has been attempted in this work. So conceived, the cortex includes the area of the septum and the entire covering of the occipital pole. Anteriorly, where the ventricles are restricted to the midline, the superficial dorsolateral surface areas together with the areas between the upper tips of the ventricles and between their anterior continuation would be included in such an attempt.

b. Apparatus

The discrimination box has proved to be one of the most satisfactory means for the study of vision in animals. In experiments using this box, the stimulus cards have marked the ends of the discrimination alleyways and the subjects, having arrived at this point have had to turn away from the stimulus card to obtain their reward. The work of Bingham (1922) and Munn (1931) on chickens, indicates that several hundred trials would have been required for the high criterion which I used in this experiment. To work with large groups of operated animals therefore, some procedure making possible more rapid learning was desired.

In the method employed, a modified Yerkes' apparatus shown in figure 3 was used.[2] The essential difference between this box and that used by Cole (1911) and Breed (1912), was that in this case the figures to be discriminated consisted in holes cut in a sheet of white cardboard (*E*). In this manner the animal went directly to the figures to be discriminated and by placing its head and neck through the correct hole, obtained food. The food behind the incorrect figure was usually covered, but when it was not, an appropriate shock was administered which easily prevented the animal from obtaining grain. As seen from figure 3, the length of the cardboard was sufficient to allow it to be slipped back and forth in its position. In this manner, changes in the position of the positive stimulus were made. The food chamber was painted black. Accordingly from the front of the apparatus, the figures appeared as dark holes cut in white cardboard.

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[2] The writer is indebted to Mr. Neil Van Steenberg for drawing the apparatus shown in figure 3.

c. Procedure

In training the birds, a preliminary period of three days preceded the actual experimentation. During this period, the animals were allowed to remain in the box for two hours daily to become acquainted with the apparatus. Both food boxes remained uncovered. By being frequently removed from before the food boxes on the first day and replaced within the starting box, the hungry birds readily learned to hasten to the food. On the second and third of these preliminary days, a three inch white

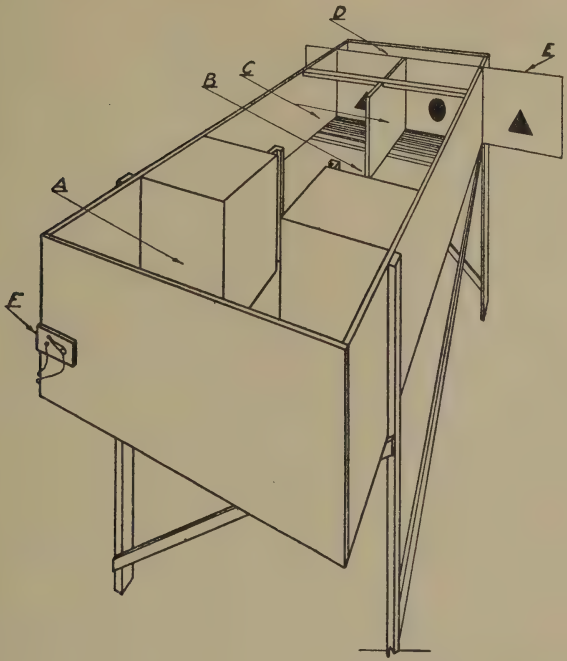


FIG. 3. DIAGRAM OF THE APPARATUS USED IN THIS EXPERIMENT

A, starting box; *B*, discrimination chamber; *C*, grid compartments; *D*, food chambers; *E*, discrimination card; *F*, switch.

cardboard was placed before the food boxes in the slit, which during training held the discrimination card. The birds had to reach over this obstacle to obtain their food during this period.

The birds were fed once daily, directly after training. Only ten trials were run each day, although the animals were still hungry when training ceased. Morning proved to be the most desirable time to train.

The chickens were individually removed from their cages and placed within the starting box of the apparatus in the same manner, location and direction, to avoid giving them a clue as to the location of the correct choice box. When they had finished a trial, they were removed from the box with the left hand, the experimenter standing to the right of the apparatus. This made for uniformity in handling the birds with the left hand while at the same time the card could be shifted and the position of the cover to the food boxes changed with the right hand. To avoid possible cues, the card was occasionally shifted back and forth several times, before the bird was replaced in the starting box.

Most chickens rapidly learned to reach through the holes in the card. As reward for a correct choice they were allowed to secure a few grains of scratch feed from the food box. No food was available from behind the negative form, for as stated above a cover was placed over this box. Nevertheless, very often on a wrong choice the chickens pecked vigorously at the cover which was preventing them from obtaining food.

Ordinarily a wire cover was placed over the entire apparatus during the first few days of training. This was unnecessary in later trials unless a severe shock was administered, in which case the chickens flew out of the box. In the initial part of this experiment, punishment was administered for a fraction of a second on every wrong choice, but later was reduced to one or two shocks for every 50 trials.

The learning criterion was set at 20 consecutive correct responses or 29 correct responses out of 30 attempts. Animals were considered to have failed when they had made 1000 trials and in this time had not reached the criterion of success. Some animals which in reality did give evidence of learning by making as high as 88 per cent correct in 60 consecutive runs were considered failures because of this high criterion. These will be considered separately in the results. A few other animals learned the problem but were considerably retarded and fell above the three sigma (620 trials) range of the controls. In later discussions these will be considered as retarded cases.

When learning had occurred, the animals ran rapidly to the positive stimulus. Several checks were then used to ascertain whether they were reacting to cues arising in connection with the discrimination card or had actually learned the problem. Thus the following were used: (1) new stimulus cards were made and used, for cards long in use always showed marks of wear; (2) the cover was removed from the food box behind the wrong stimulus; (3) occasionally the food box behind the correct figure was covered and that behind the incorrect form left open (this caused the birds to pace back and forth between the discrimination chamber and the covered food box); (4) the card was at times, shifted quickly while the animal was hastening over the discrimination chamber (a shift in the animal's direction was interpreted in this case to indicate discrimination on the basis of vision); (5) lastly, some birds after learning required coaxing to enter either alleyway when the discrimination card was removed or a narrow three inch cardboard substituted in its place.

Several other checks were made during training to avoid the possibility that the animals might pick up a cue. Thus I sometimes turned my back toward the apparatus and observed the animals with a mirror. Extraneous noises were minimized as much as possible or were at least constant in position. The brightness of the two alleyways was as nearly constant as possible since the apparatus was placed directly before and in the center of a large window. Lastly, other experimenters have trained the animals after learning had occurred without any effect upon the animals' ability to discriminate.

d. Animals

The chickens were all young pullets approximately nine to twelve weeks old when purchased. White leghorn pullets were preferred because of their activity, but during the winter months these could not be obtained and nineteen barred rocks were substituted. Examinations of both the objective records and the lesions showed no difference between these two groups.

The food used as incentive was a combination of yellow cracked corn, wheat, barley and milo maize. Besides this ration of hard food obtained as a reward, growing mash mixed with a little water was given just after training. At first, cod liver oil was mixed with the mash, but later it was given directly with an eye dropper three times a week. Lettuce and meat were also given when available.

e. Operative technique

In attempting to localize the area for pattern vision in the chicken cortex, I tried to make a survey of the surface of the whole forebrain. The method used consisted in destroying various areas of brain tissue under consideration. The subject was etherized, feathers clipped, scalp longitudinally slit, skull trephined, and tissue destroyed with an electric cautery. The whole procedure was performed under aseptic conditions. Both hemispheres were operated upon simultaneously. An attempt was made to produce symmetrical, bilateral lesions. The scalp was closed by interrupted sutures and a celloidin bandage applied to prevent scratching of the wound. In most cases, after two weeks the birds were entirely recovered. They were then started in the discrimination apparatus. A few, because of severe lesions had not recovered after several weeks, and five were fed by hand for a considerably longer period than the time required by the average operative case to recover and learn the problem.

f. Histological procedure

Having learned or failed to discriminate, the animals were brought to necropsy. Their brains were fixed and hardened in 95 per cent alcohol, imbedded in celloidin and sectioned at 50 μ. Every fifth section was saved. In this manner four sections were obtained per millimeter. A series of sections was cut covering the entire area of lesion in both hemispheres. About half the brains were stained in iron hematoxylin, the other half in thionin. The sections showing lesions were drawn under camera lucida and the extent of lesion determined under high power and marked on the drawings. From these drawings a composite picture of the lesion was obtained showing the actual extent of destruction on the surface of the brain (plates I to V).

The primary purpose of this project was to investigate cortical activity in relation to pattern vision. Depth of lesion was thus very important, because the cortex is superficial except in the septum where some of it is far removed from the dorsal surface. In the reconstructed lesions shown in plates I to V, I have attempted to show depth by using three different markings: (*a*) stippling, (*b*) black parallel lines, (*c*) total black. Lesions were considered shallow when they did not involve more than the cortex. In the septum where the cortex is thick, lesions were considered shallow when they did not extend to a depth greater than six cells. These lesions are represented by stippling. Lesions that destroyed the forebrain material below the cortex but in which the lesions did not reach to a depth of one half the forebrain are shown in parallel black lines. Such lesions destroyed the upper cortical layers and may have pierced almost to the paleostriatum. The deepest lesions are indicated by the total black areas and represent regions in which the destruction or degenerative changes are found to a depth of at least one half the forebrain. One further marking is found in a few sections. Occasionally degenerative changes were found to have undercut surface areas which showed no lesion. These were usually small areas and have been indicated in the diagrams of plates I to V by small circles. Most dorsal surface lesions show only small destruction when viewed laterally. However when deep dorsal lesions occur and are viewed from the side, the lateral surface appears intact but undercut. This accounts for the large areas of circles in some reconstructions.

V. EXPERIMENTAL DATA

a. Learning by normal birds

Ten unoperated white leghorn pullets learned the problem. With but one exception the records for these animals all fell below 320 trials and 100 errors. As seen in table 1, the range is from 119 to 498 trials with an average of 256.9. The errors range from 49 to 155 with an average of 82.8.

Six of these animals were tested for retention two weeks after meeting the criterion. With only one exception, retention was perfect.

TABLE 1

Summary of training records of normal animals

CHICKEN	TRIALS	ERRORS
1	498	155
2	300	88
3	320	97
4	262	90
5	242	83
6	140	50
7	264	87
8	272	73
9	119	49
10	152	56

b. Learning by operated birds

Out of 50 operated birds only 6 failed to reach the high criterion of 20 consecutive errorless runs, or one error in 30 trials. The records of these animals are given in table 2. Column S shows the total area of destruction (lesions in both hemispheres summed for the single figure). Column DS shows the total area of lesion weighted for depth. Trials and errors are also presented.

The surface reconstructions of the cerebral lesions in these animals, together with typical cross sections are found in plates I to V. The arrangement of cases in table 2 and in plates I to V has been made on the basis of trials. This has placed all the failing cases together. An arrangement based on errors would

TABLE 2

Summary of training records of animals with forebrain lesions

S = total surface area of lesion. DS = total area of lesion weighted for depth. Tr. = trials. Er. = errors.

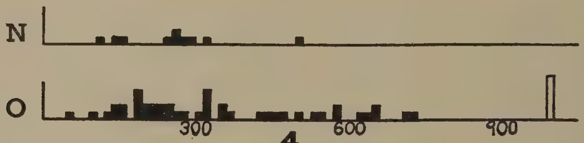
NUMBER	S	DS	TR.	ER.	COMMENTS
1	28	30	60	16	
2	79	106	93	35	
3	43	63	135	42	
4	24	24	141	39	
5	35	66	141	63	
6	34	39	158	57	
7	51	78	163	60	
8	85	194	181	75	
9	54	85	185	36	
10	61	93	187	66	
11	35	55	188	56	
12	61	101	205	85	
13	30	99	206	109	
14	39	49	212	82	
15	80	84	221	73	
16	52	87	234	90	
17	45	85	234	91	
18	79	124	252	73	
19	33	52	252	85	
20	47	73	256	61	
21	66	91	276	109	
22	35	69	312	122	
23	89	143	316	112	
24	80	162	316	147	
25	41	53	321	78	
26	83	122	322	109	
27	36	62	353	101	Made 90 per cent correct by 80th trial
28	27	27	357	100	Made 90 per cent correct by 200th trial
29	46	102	364	118	
30	54	70	428	203	
31	56	73	437	188	
32	56	71	462	219	
33	97	237	480	171	Made 90 per cent correct by 240th trial
34	59	75	507	211	Animal was very lazy
35	60	123	526	182	Made 93 per cent correct at 330 trials
36	78	181	542	212	Had leg weakness
37	52	84	576	207	
38	31	38	578	287	Had roup at one time
39	50	89	631	248	
40	42	49	637	271	Frightened at trial 350
41	129	321	655	352	
42	82	179	665	299	
43	132	306	711	375	

TABLE 2—*Concluded*

NUMBER	S	DS	TR.	ER.	COMMENTS
44	102	231	727	220	
45	39	79	1,000	360	Made 88 per cent correct, trials 490–550
46	74	126	1,000	388	Made 84 per cent correct, trials 620–680
47	122	268	1,000	462	Made 80 per cent correct, trials 510–540
48	52	85	1,000	500	Animal frightened and erratic
49	86	180	1,000	598	Animal listless and anemic
50	50	88	1,000	510	No indication of learning

have only slightly altered the arrangement for there was a rank order correlation of .943 between trials and errors.

Variation in learning is shown in figure 4, where the normal and operated animals are compared as to trials required in learning



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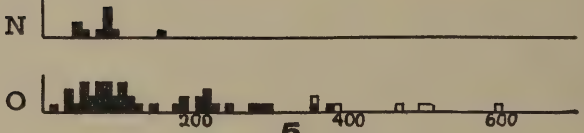

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FIG. 4. DISTRIBUTION OF NORMAL (*N*) AND OPERATED (*O*) ANIMALS AS TO TRIALS REQUIRED

Black areas indicate animals that learned; unfilled areas those that failed

FIG. 5. DISTRIBUTION OF NORMAL (*N*) AND OPERATED (*O*) ANIMALS AS TO ERRORS MADE

Black areas indicate animals that learned; unfilled areas those that failed

the discrimination. The animals which failed are indicated on this chart with unfilled squares whereas total black squares indicate those which learned. Figure 5 is a comparison of operated and unoperated chickens with respect to errors made, and here again unsuccessful cases are represented by open white squares.

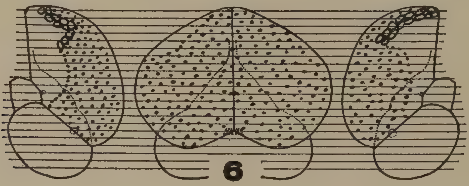
These histograms show that the normal animals were superior to the operated animals both as to trials required and errors made.

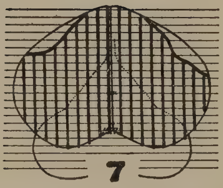
1. Animals learning within the lower 75 per cent range of normal animals

A cursory glance at plates I to V indicates that all the dorsal and most of the lateral surface regions have been destroyed at least superficially. A composite diagram showing the entire area of destruction in those animals which learned within the range of the lower 75 per cent of normal chickens (that is up to 339 trials) is seen in figure 6. With the exception of a small bit of tissue on the lateral anterior sides, the entire dorsal surface has been explored in these animals. The first 26 animals of table 2 are included in this group. Since these animals learned as though they were normal, the characteristics of their cerebral ablations are important. Animal number 8 of this group learned in 181 trials, well below the average for unoperated chickens, and yet the lesion shows most of the posterior cortex destroyed, together with very deep accompanying destructions. Chicken number 13, with lesion destroying much of the anterior cortex not destroyed in the case of number 8 is also included within this group. Thus in two animals, most of the posterior and central anterior cortex is destroyed together with the underlying striatum, with little or no effect on vision. By inclusion of the other 24 cases of this group, the total surface area destroyed is increased to the proportions indicated in figure 6. Figures 7 and 8 are composite drawings of the medium deep and deep lesions respectively in this group of operated, but normally behaving animals. From these three figures (6, 7, 8) two facts stand out prominently. In the first place, the total extent of surface area explored is almost as great as the surface area of the brain; and in the second place, the deepest lesions occurring in this group of 26 animals are largely confined to the posterior half of the brain. These results demonstrate that the capacity for detail vision may survive the destruction of every part of the cortex of the bird, even when the lesions are of considerable magnitude. They do not substantiate the opinion that the occipital pole is visual.

2. Animals much retarded in learning

There are 12 animals, number 27 to 38, which learned the problem, but in point of behavior records they fell above the 75th percentile (339 trials) and below the three sigma mark (620 trials) of the normal animals. This is a range not beyond the normal probability of occurrence. However, when it is remembered that only 26 animals occupied the lower 75 per cent of the distribution, there is suggestion of a retardation other than chance. On observing the reconstructed lesions (plates III and IV) of these 12 animals, one sees that they scatter over the whole surface of the diagrams, and have nothing more in common than those which learned more rapidly. The only explanation which I can offer for the fact that so many cases fall in this range is that the lesions produced a mild dementia which in turn reflected on the behavior records.





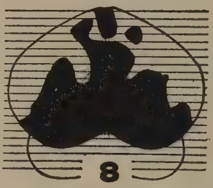


Fig. 6. Combined Surface Lesion of Operated Animals Learning Within the Range of the Lower 75 Per Cent of Normal Cases

Fig. 7. Combined Medium Deep Lesions of Operated Animals Learning Within the Range of the Lower 75 Per Cent of Normal Animals

Fig. 8. Combined Deep Lesion of Operated Animals Learning Within the Range of the Lower 75 Per Cent of Normal Animals

Above the three sigma mark of normal animals, there are six other chickens which learned (numbers 39 to 44). The main characteristics of the lesions in these subjects are that they are relatively large and posterior. I believe that size, rather than locus of injury, explains the retardation of these animals since there is reason to suppose that more severe dementia would result from larger than from smaller lesions.

3. Cases failing within the training period

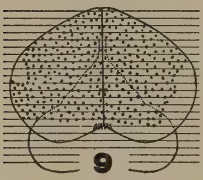
We saw previously that practically all surface areas were destroyed without any noticeable effect upon vision. There were however, six animals (45, 46, 47, 48, 49, 50) which did not reach the criterion of success in 1000 trials. Two of these animals gave evidence of discrimination: chicken 45, which eventually ran 88 per cent correct in 60 consecutive trials, and chicken 46, which made 84 per cent correct for the same number of successive attempts. Of the other four animals, number 47 reached an efficiency of 80 per cent correct for 30 consecutive runs. Later, this animal became frightened and failed. Animal 48 became frightened quite early in training and never overcame her fear. Case 49 was in poor physical condition most of the time. The remaining animal, number 50, alone never gave any sign of learning the problem. She was not ill at any time.

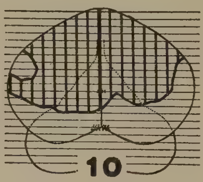
In view of the above considerations we could dismiss the first five failing cases as either discriminating, or failing, due to poor health or fright, and conclude that only one animal really failed. However, as this procedure would be radical we shall consider these cases in more detail.

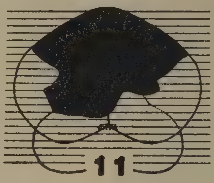
If for a moment one refers to figure 5 where the error records of the birds are shown, it is readily seen that two animals (45, 46) had error records comparable to the worst of the cases which satisfied the criterion of success. This indicates again that these two animals could discriminate. A third doubtful case as mentioned above is animal 47. As the error record of this animal was fairly high, I shall consider it together with animals 48, 49 and 50 as failures.

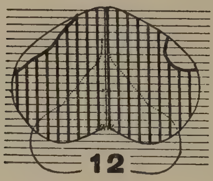
A composite diagram of the lesions of these four animals is seen in figure 9. This figure shows two main facts. In the first place, the posterior and postero-lateral areas are uninjured. This again is in disagreement with the statements in the literature that the posterior pole in birds is visual. In the second place, it is seen that with the exception of the occipital pole and the lateral occipital areas, the regions explored in the failing cases are identical with the regions explored in the successful animals.

Analyzing these four cases in search of some similar cause for their failure, the depth of lesion must be considered. Figure 10 shows a composite lesion of medium depth while the composite deep lesions are represented in figure 11. For comparative purposes figures 12 and 13 are diagrams of the lesions of all successful animals and represent the combined medium and deep lesions of these cases. It can be readily seen that there is much overlapping. In the medium type of lesion there is a little antero-lateral tissue destroyed in the cases that failed to reach the criterion (fig. 10) that is not destroyed in the cases that were successful (fig. 12). However, this area is found in only one of the failures









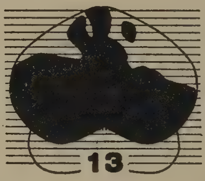


Fig. 9. Composite Diagram Showing Total Extent of Surface Explored in Animals Which Failed

Fig. 10. Combined Medium Deep Lesion of Animals Which Failed

Fig. 11. Combined Deep Lesions of Animals Which Failed

Fig. 12. Combined Medium Deep Lesion of Animals Which Learned

Fig. 13. Combined Deep Lesion of Animals Which Learned

(47). The same follows for figures 11 and 13. In the case of these deep lesions, much more anterior tissue is destroyed in the failures (fig. 11) than in any of the successful animals (fig. 13). Here again it was the same animal (47) which showed a unique lesion that was not paralleled by a similar lesion in any of the successful cases. In consideration of the training record of this animal, the probability that the unique deep regions destroyed in this case are the essential areas for pattern vision while admissible, is remote.

A composite lesion of areas common to all the four failing cases is found in figure 14. It can hardly be possible that these two areas are the essential regions for pattern discrimination per se, for after a consideration of animals 2, 10, 13, 35 and 41 we see that these areas have been destroyed in cases which learned readily.

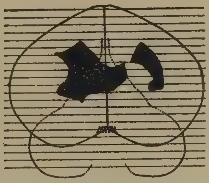


Fig. 14. Common Area Destroyed in Cases Which Failed

In view of the above considerations, it is quite apparent that there was no single area of the brain destroyed in these unsuccessful cases which could have caused failure. Only animal 47 had an area unique to itself and as stated before, this bird gave some evidence for discrimination.

4. Animals learning with striatal lesions

Thus far in this paper, little consideration has been given to particular striatal nuclei, except to group them into the deep or medium category. I shall consider them briefly at this point. An attempt has been made in figure 15 to project roughly some of the larger forebrain nuclei onto the dorsal surface. The location of these projected masses will vary with the points chosen for projection. Furthermore, depth of structure cannot be shown. Thus the posterior tip of the accessory hyperstriatum is very thin, but in the anterior areas it extends to the base of the brain. The six levels indicated in figure 2 are also indicated on figure 15 for orientation. By superimposing the diagrams of plates I to V upon figure 15, a rough idea can be obtained of the subcortical structures involved in the lesions.

Two animals (41, 43) with all the striatal masses posterior to the anterior commissure destroyed, learned the problem. The archistriatum and half of both the paleostriatum and neostriatum were destroyed in these animals. The lesions in cases 13, 19 and 22 are medially located and have destroyed most of the accessory hyperstriatum. Nevertheless, vision functioned normally in these animals. The remainder of the forebrain masses, the hyperstriatum, the anterior parts of both the paleostriatum and neostriatum were invaded in other cases, without noticeable effect on the ability to form the visual discrimination habit. The lesions in each case were small and no combined lesion would show all of these areas destroyed. These anterior nuclei were all invaded, and for the most part destroyed in one case (47), and this animal did not learn. Accordingly, there are subcortical areas in the anterior region that were not abolished in successful animals, that were in one animal that failed. The inference seems to be that whereas huge subcortical lesions in the posterior pole do not abolish vision, huge subcortical lesions in the anterior areas do.

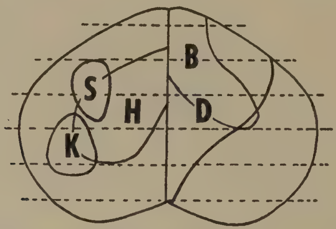


Fig. 15. Projection of Some of the Main Striatal Nuclei onto the Dorsal Surface of the Forebrain

For significance of lettering see figure 1

5. Extent of lesion in relation to retardation

According to the results, no distinct area such as we find in mammals seems to be critical to pattern vision in chickens. Some other system must have developed in birds which serves the same purpose in them, that the visual area does in mammals. In search for such a system in the forebrain of birds, I have followed up two possibilities. The first was that vision is correlated with mass of cortex in the bird.

To determine this, the planimeter was used to measure the total area of the lesions and these were then correlated by the rank order method with trials required to master the problem. If the formation of the visual habit was dependent upon mass of cortex, correlating total surface area destroyed in each hemisphere with behavior records should have given a significant figure. The results were low, a correlation of only + .22 ±.09 was found.

There was another possibility in connection with mass effect. Formation of the visual habit might be correlated with mass of the whole forebrain. To determine this, two other planimeter readings were taken; one measured the areas for the medium deep lesions and the other those for the deep destructions. The former of these two was given double weight and the area for deep lesions was given a triple weighting. These weightings together with the planimeter readings for the total surface areas were then summed and this sum was correlated in the same manner as above with trials. The result in this case was +.39 ±.08. This figure is low, yet it is higher than the correlation between surface area destroyed and trials.

There is an indication in these results which shows that large surface lesions tend to be more detrimental to the visual problem than small lesions. There is a stronger tendency which indicates that the formation of the visual habit is dependent upon total mass of forebrain tissue as a whole. However, as previously mentioned, destruction of cerebral tissue may produce a dementia for learning which prevents formation of a visual habit, although vision may remain. Again, cerebral ablations may produce inertia in the animals and thus favor failure.

6. The possibility of a dual control

Another possibility for a central visual mechanism is that the bird might have some sort of dual control for vision in the forebrain, and that to destroy vision, both these controlling areas must be destroyed. In figure 14 we saw that there were two areas common to all failing cases. Parts of these, rostral to the anterior commissure are bilaterally symmetrical with two common areas as represented in figure 16. If these areas per se, were the cerebral visual controlling mechanism, then in all animals with these areas destroyed detail vision should be wanting. Yet in connection with figure 14 we found animals 2, 10, 13, 35 and 41 that had lesions in these regions and detail vision still existed.

There is a further possibility, inasmuch as these common areas together may represent only one part of a vicariously functioning system. The failures not only had these common areas ablated but they also showed some, if not considerable destruction of other anterior areas. It may be possible then, that a certain amount of cerebral mass with indefinite locus rostral to the anterior commissure plus the areas shown in figure 16, which when destroyed will produce a deficiency of vision as shown by failure in pattern vision tests. More cases are needed to settle this possibility.

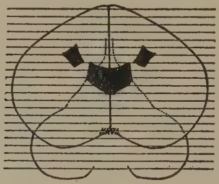


Fig. 16. Bilaterally Symmetrical Areas Common to All Animals Which Failed

VI. DISCUSSION

The training records for both trials and errors in the operated animals showed considerably more dispersion than those of the normal animals. The lesions were scattered over the whole surface of the forebrain, but there was no consistency found between the loci of lesions and retardation in learning. This may mean that lesions in any region merely accentuate the normal variability existing among the animals.

The existence of a cortical retina, or even of a combination of cortical areas which when destroyed, would abolish detail vision, was not found. This pushes the search for a visual correlating center down into the forebrain nuclei, if not into the diencephalon. Certainly the posterior striatal nuclei are uninfluential in the perception of detail vision. The anterior striatal nuclei were all separately invaded in various animals which learned, but they were all invaded together in one animal which failed to reach the criterion. This suggests that destroyed together they would prevent the formation of visual pattern habits, whereas when individually destroyed they would not.

One writer (Elliot Smith, 1919) considers the accessory hyperstriatum as the primordium of the neopallium of mammals. That this neopallial area in its entirety may be the essential area for pattern vision is indicated by the results obtained on animal 47. As stated above, this animal with all this area destroyed failed, whereas those animals with just invasion into the area, learned.

We know that brain tumors, hydrocephalism, cerebral wounds and the like, produce a dementia in human beings. We also know that by certain destructions in the human brain, intelligence may be lowered and vision remain intact. The same may be true of chickens. Capacity to learn may have been effected without detriment to vision.

Phylogenetically, we find an increasing neural organization from lower to higher animals. In mammals, a highly developed visual system in the forebrain is found. This is not so in birds, even though both phylla have branched from reptiles. One hypothesis which might explain this lack of a visual cortex is the belief that birds have developed from a different reptilian branch than have mammals and as a result the disposing tendencies to development may have differed and a highly developed cortex result on the one hand, whereas on the other it would not have developed or would have developed only slightly. This idea however is not supported by the evidence as found by Craigie (1929b) that in the more primitive birds such as Apteryx, more cortex is found than in the more developed birds. This suggests that evolution in avian forms has followed a course different from that in mammals and that after a certain complexity of cortex had been developed, instead of developing more complexity it has actually degenerated in importance and that structures have assumed importance in birds which in mammals are less influential or non existing. The hyperstriatum complex may be one of these more important areas in birds. Another area, and one which we believe is connected with vision in mammals, is the mid brain. It is certainly a region of relatively high development as judged from external size. Yet what part the mid brain or optic lobes, play in avian vision is a question yet to be settled.

VII. SUMMARY

Cerebral injuries were performed on 50 chickens, after which they were trained on a modified Yerkes-Watson discrimination apparatus in a test for evidence of pattern vision.

1. All regions of the cortex were destroyed. No area of this superficial covering was found essential to the formation of the discrimination of visual patterns.

2. Contrary to the results of workers on mammalian forms, it was found that the cortex is not essential to vision. However, if the lesions were sufficiently large, a defect in learning the visual problem was apparent, and feeding reactions were slower. I believe that this is not so much a visual defect as it is a lowering of the general intelligence of the subject.

3. Both large (superficial) and deep lesions in any region were more deleterious to learning than smaller lesions in any region. This points to some sort of a mass effect of cerebral tissue in the formation of this visual habit. Posterior lesions showed this tendency quite uniformly but there were several discrepancies in the anterior regions. The correlation between superficial area destroyed and trials was +.22 ±.09. The correlation between depth of lesion or volume of tissue destroyed, as determined

by a purely arbitrary method of weightings, and trials was +.39 ±.08.

4. Six out of fifty cases failed to reach the criterion of success. Two of these gave evidence of discrimination. The lesions of the remaining four failures were located mainly in front of the anterior commissure, but as many successful cases showed lesions in these same regions, destruction of the anterior region per se, did not cause failure to learn.

5. An area common to all the failing cases was found. As there were many cases which learned with lesions in this same region, destruction of the area itsef was not the cause of failure in these four cases.

6. Some basal nucleus or combination of basal nuclei in front of the anterior commissure may influence the interpretation of visual signs. Only by multiplication of cases can this be determined.

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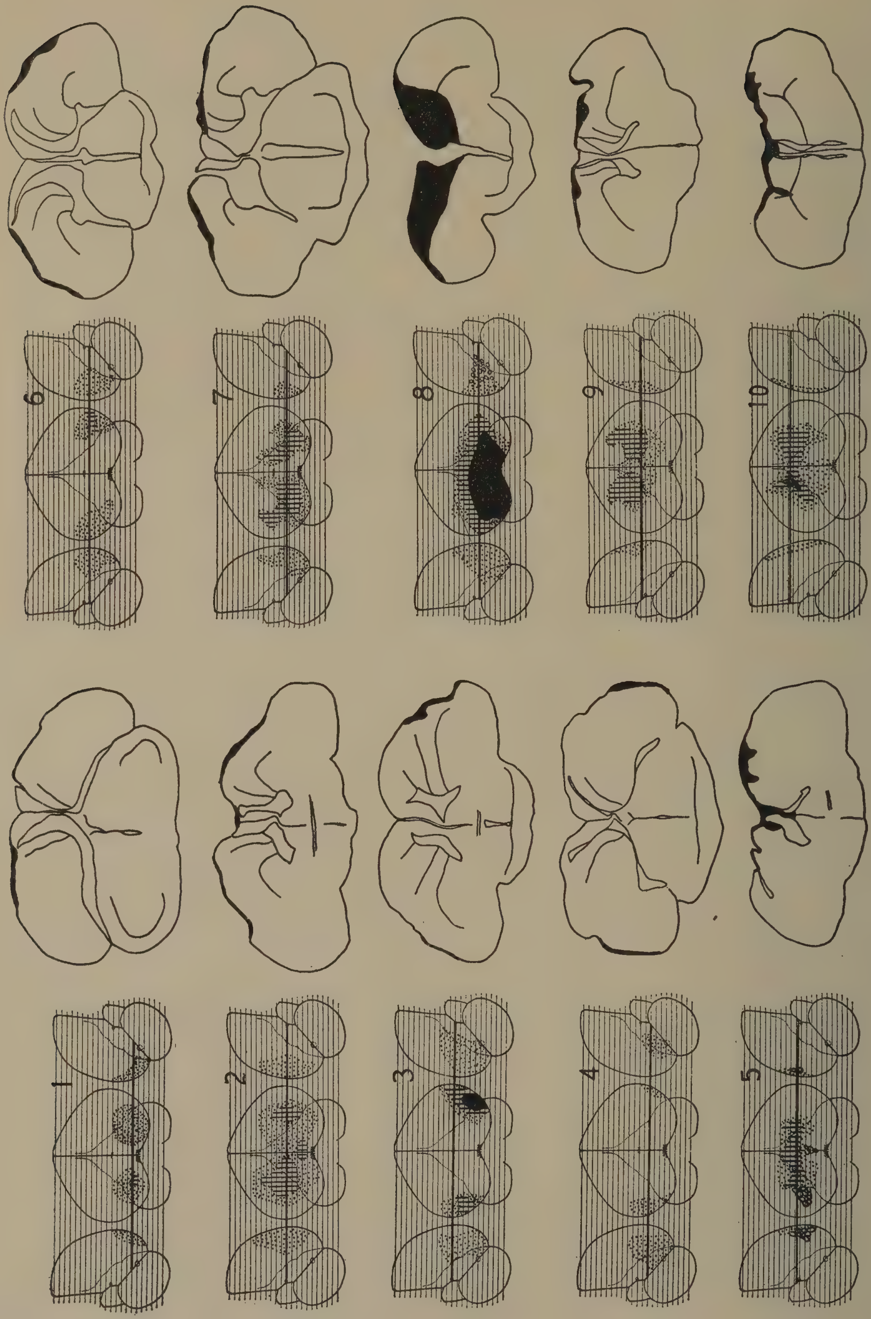
EXPLANATION OF PLATES

The reconstructed lesions of the 50 operated animals are found in plates I to V, which show a dorsal and a lateral view of each brain. To the right of each reconstructed case are typical cross sections through the center of the lesion. The numbers on the dorsal views refer to the number of the animal. Four kinds of markings have been used: (1) solid black, representing either areas of deep lesions on the surface diagrams, or degenerated areas in the cross sections; (2) parallel vertical lines, representing the medium deep lesions; (3) stippling, representing surface lesions and; (4) small circles, representing undercut areas.



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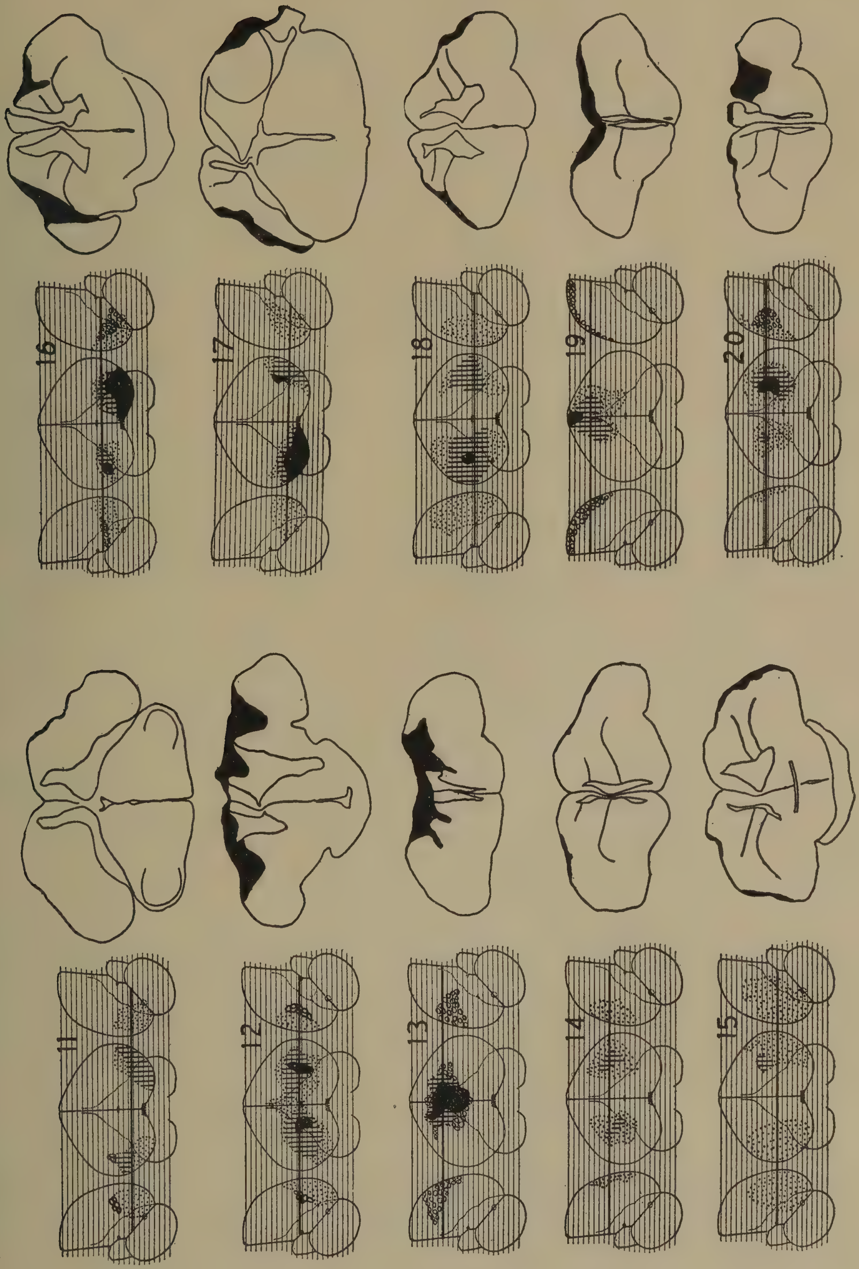

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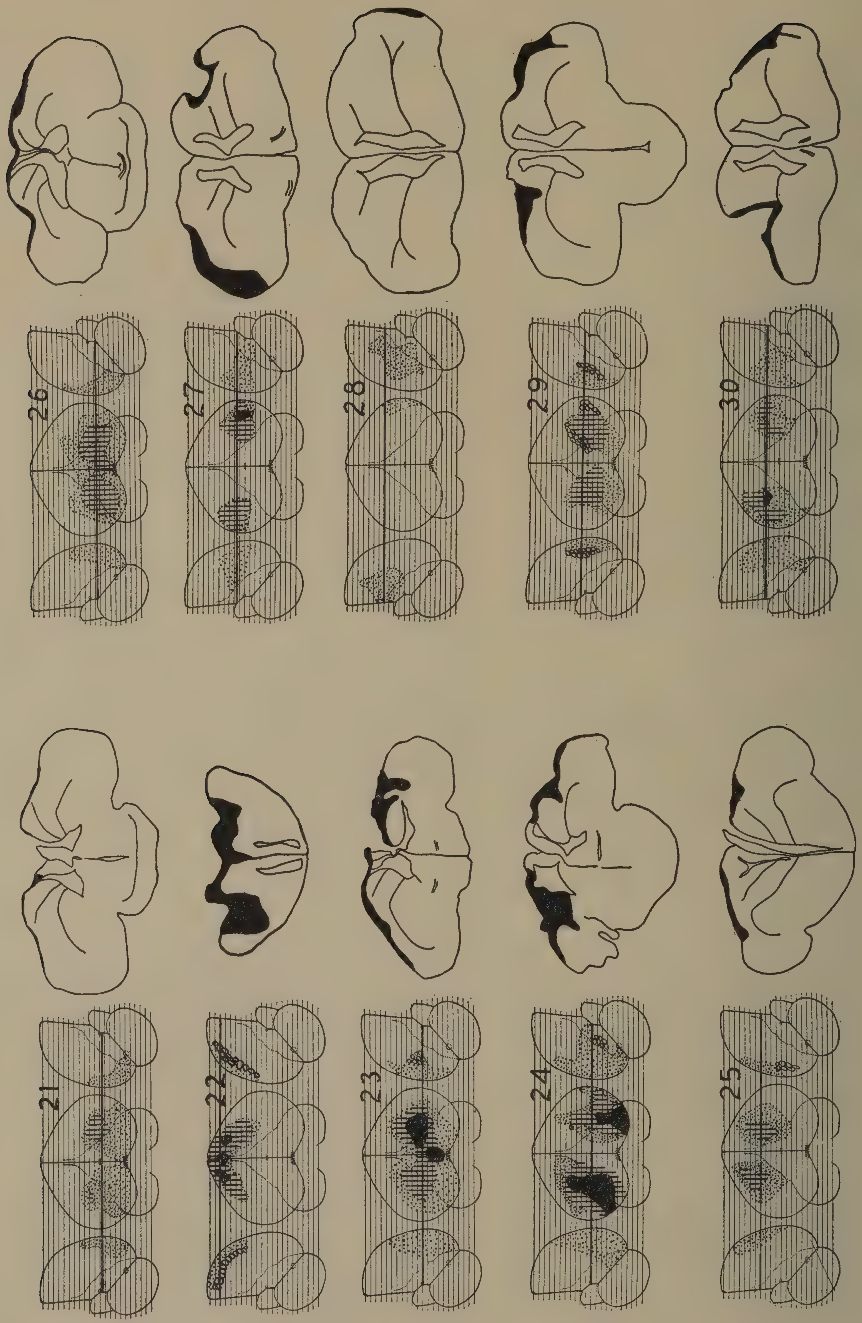

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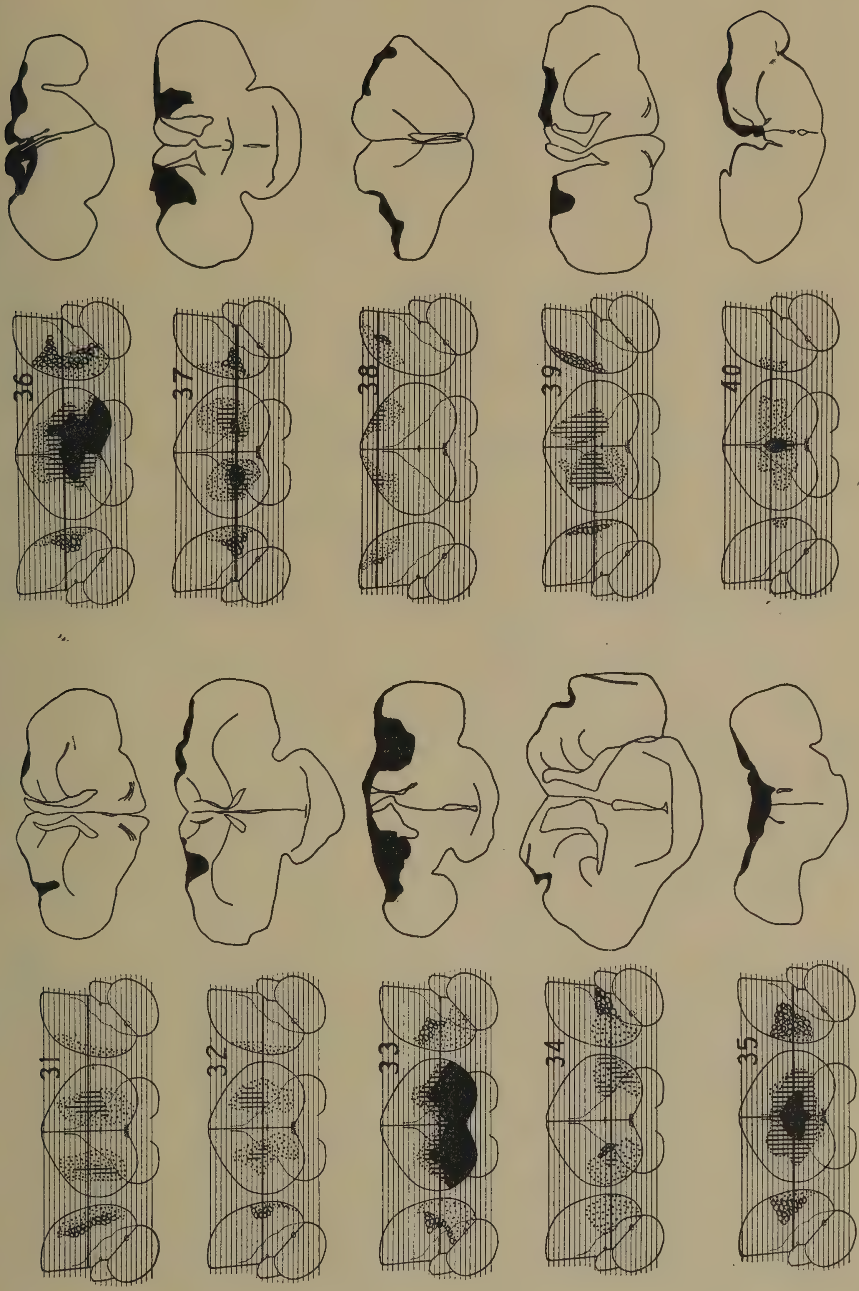

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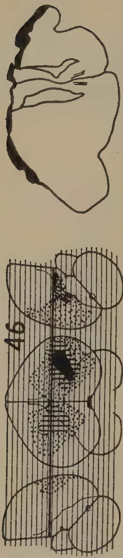
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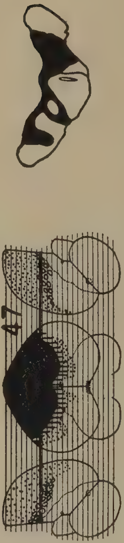
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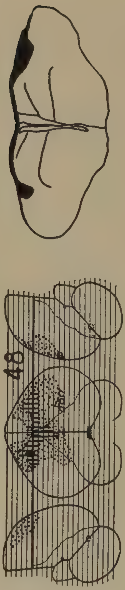
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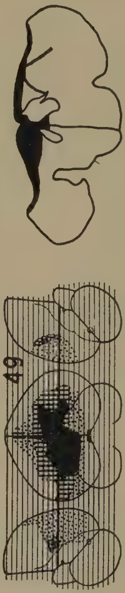
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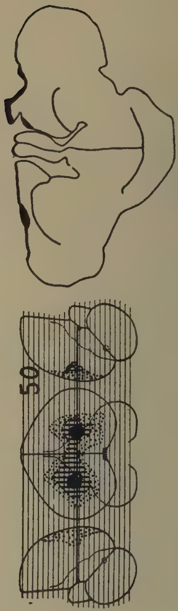
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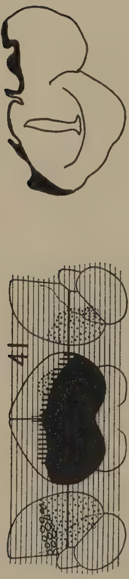
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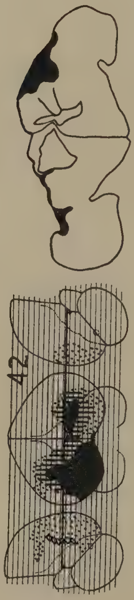
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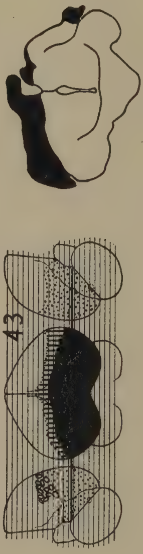
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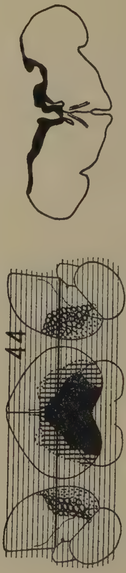
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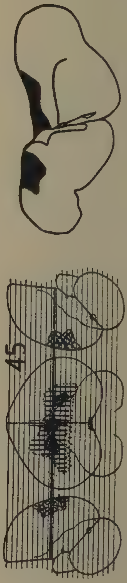
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INFANT BEHAVIOR

BY
MANDEL SHERMAN, IRENE SHERMAN
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BALTIMORE, MARYLAND, U. S. A.

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INFANT BEHAVIOR

MANDEL SHERMAN, IRENE SHERMAN AND CHARLES D. FLORY
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INTRODUCTION

The plan of this study was to observe the behavior of new-born infants under relatively controlled conditions, utilizing stimuli of variable intensities. Discrepancies in the reports of various experimenters are in part due to the lack of standardization of apparatus and stimuli. For this reason, a great deal of preliminary work was done in order to construct apparatus by which known and variable intensities of stimulation could be applied. This apparatus is described in Chapter I.

We are under great obligation to Professor Donald Slesinger and the Social Science Research Committee of the University of Chicago for the funds which made the investigation possible. We wish to express appreciation to Dr. Fred L. Adair, Chairman of the Department of Obstetrics and Gynecology for his interest in the problem and for the arrangements at the Chicago Lying-in Hospital; also to Miss Pearl Braithwaite, Superintendent of the Hospital, for arranging the working facilities. Through the patience and efforts of Miss Emma Kelting, Superintendent of

Nurses, it was possible to examine a large number of infants and to obtain the nursing assistance which was a vital part of the experimental conditions. We are also obliged to Dr. Joseph B. DeLee for his many favors. Throughout the investigation our work was facilitated by the constructive attitudes and personal help of the nurses and supervisors who were at all times ready to aid us.

Thanks are extended to Professor Harvey Carr, Professor Frank N. Freeman and Professor Charles H. Judd for reading the manuscript and for their many constructive suggestions, and to Professor Nathaniel Kleitman for aid on Chapter X.

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CHAPTER I

THE EXPERIMENTAL CONDITIONS

Identical stimuli applied with different intensities may produce quite different responses. This has been amply shown by Genzmer, Carmichael and others in eliciting responses of the fetuses of animals, and by Sherman of newborn infants. Some experimenters, like Bühler, claimed that "artificial" stimuli should not be applied to infants, on the supposition that we can learn the nature of an infant's development only when we observe his spontaneous reactions. It is needless to say, however, that there are no "spontaneous" activities of infants in the sense that external stimuli have no influence.

The problem of the proper technique in work with newborn infants reduces itself to three phases: the control of the conditions under which experiments are conducted; the application of constant and measurable stimuli to an adequate number of subjects; and the accurate description of the responses to the various stimuli applied with different intensities.

The following is a description of the conditions under which the experimental work was conducted, the nature of the apparatus used, the methods of applying the stimuli, and the general techniques of measuring the responses.

EXAMINING ROOM

The infants were examined in a room approximately 10 feet by 16 feet adjacent to one of the nurseries in the Chicago Lying-in Hospital. The experimenters had exclusive use of the room during the course of the investigation. There were two outside windows facing the East, but a five-story wing of the hospital projected in such a manner that direct sun rays were eliminated. Shades were drawn to cover the top half of the windows. Large glass partitions on either side of the door provided some indirect light from the corridor. The light was bright enough to provide satisfactory working conditions, yet subdued enough to permit experimentation under relatively normal conditions. Although the experimental room was somewhat darker than the nursery, it is the judgment of the experimenters that the responses elicited were not influenced to any significant degree by the illumination. Lighting conditions were quite comparable from day to day.

A check was made of thermometer readings at frequent intervals until it was determined that the experimental room could be kept at practically a constant temperature with little difficulty. A minimum of 80° and a maximum of 84° were the limits used in the experimental room. Since the subjects were always examined without clothing, it was felt that the temperature should be kept at the level used in the hospital work rooms. If for any reason the temperature failed to reach a minimum of 80°, work was suspended for the day. An excessive temperature was reduced by outside air through a gravity ventilating system.

Examinations were made for the most part between 10:00 a.m., and twelve noon. Infants were fed at four-hour intervals, with 10:00 a.m. as one of the feeding periods. Subjects were brought to the experimental room after their 10:00 o'clock feeding. A few infants were examined before they had been to breast, since some of the examinations were made before 10:00 a.m., and on three afternoons. Feeding is relatively an unimportant factor during the first hours of life since the amount of nourishment received is negligible. Once the feeding routine has been established it is important, however, to make sure that subjects have had their hunger satisfied before experimentation begins, if the influencing factor of hunger is to be controlled.

All examinations were made with at least two experimenters and a nurse present. When the experimenters were ready the nurse brought an infant to the experimental room. Subjects were selected at random. Factors of age, sex, wetness, dryness, asleep, awake and quiet were disregarded in selecting a subject. The nurse was instructed to bring any infant. A subject was lifted from the crib, carried to the experimental room, the clothing removed, the child wrapped in a blanket, and placed on the examining table. Ordinary quilted padding and a sheet covered the top of the table. The examining table was placed about three feet from the outside windows with the length of the table parallel to the width of the windows. Subjects were placed with their heads toward the windows so that they lay with the eyes away from the light.

If a subject were not awake when he arrived in the experimental room he was aroused before the stimuli were applied. It was often a difficult task to keep an infant awake and at the same time keep him quiet, especially when stimuli of various types were being applied. The threshold was much higher in some infants than in others. The possibility of upsetting an infant emotionally varied significantly from subject to subject. If an infant became emotionally aroused or remained asleep continuously it was impossible to give some of the stimuli. It was futile, for example, to apply a pain stimulus to a crying infant; likewise one could tell nothing about eye-movements in a sleeping child.

LIGHT STIMULI

Two types of eye responses have received considerable attention in studies of infants; namely, the pupillary reflex and eye movements. If these reactions are to be studied experimentally it is necessary to provide stimuli which are adequate, that is, neither too strong nor too weak. The dearth of apparatus suitable for work with newborn infants required the construction of instruments to suit the needs of the investigation. A special lamp, shown schematically in figure 1, was constructed for the experiment.

A 6.3 volt frosted Madza 40-T-3 miniature screw base lamp was connected in series with a rheostat having five selector stops. Current was supplied by a toy transformer with 115 volt primary and selector switch giving six different secondary voltages. This apparatus made it possible to give constant stimuli of different intensities. Calibration of the apparatus in terms of foot-candle illumination intensities was obtained by a special Weston Photronic Cell placed opposite the tube opening at an optical distance of 2 inches. Lamps were changed frequently to reduce the slight decrease in illumination resulting from use.

Preliminary experimentation revealed that transformer position

1, and rheostat position 3 (recorded as 3 c.p.) was about the lowest light which would produce satisfactory pupillary contractions with infants near the end of their stay at the hospital. Readings at 3 c.p. were found to equal three foot-candles in intensity at an optical distance of 2 inches. Transformer position 1, and rheostat position 4 (6 c.p.) gave a foot-candle intensity of 5.94 or practically 6. Transformer position 3, and rheostat position 3 (12 c.p.) gave a foot-candle reading of 11.96, or practically 12. These three positions proved to be most satisfactory and were used throughout the investigation to elicit pupillary reactions and eye movements. The effectiveness of these stimuli in discriminating developmental differences will be shown when the data are presented.

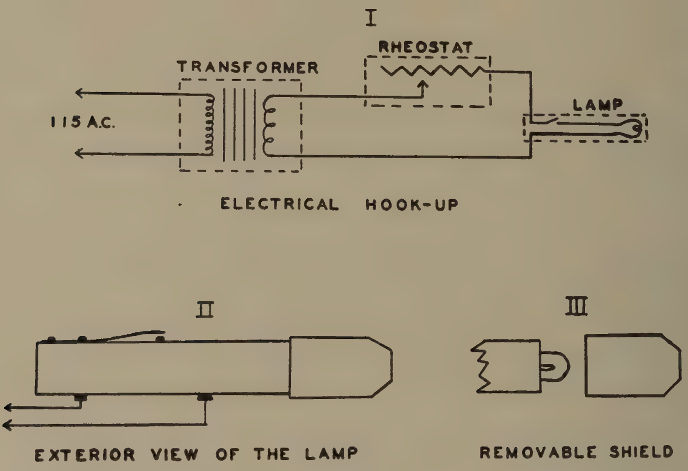

FIG. 1. SCHEMATIC DRAWING OF APPARATUS FOR OBTAINING EYE REACTIONS

Pupillary reactions of newborn infants are variable to ordinary light. Some infants upon arrival in the examining room had very large pupils; others at a comparable age had very small pupils. If the eyes are forced open the pupils of some infants are large while others are quite myotic. These differences in pupillary size indicate that experimenters must exercise extreme care when interpreting the reactions to light stimuli. It was therefore decided that the infants were to be kept awake for a period sufficient to insure accommodation to ordinary light. A nurse always stood between the window and the infant for a minute or more before the light stimulus was given. The light was thrown into the eye at an angle of approximately 45°. The aperture of the lamp was held approximately 2 inches from the cornea. It was the practice throughout the study to begin with the lowest degree of light (3 c.p.) and increase the intensity until a good response was observed or until a stimulus equaling twelve foot-candles of illumination had been given. The reactions were recorded as no response, fair, or good. Two observers noted each reaction. Complete agreement was demanded before a record was made as final. Contractions which were easily observed yet not wholly adequate were recorded as *fair*. A *good* response was recorded when the reaction was adequate both in speed and in amount of contraction.

Sufficient data have been assembled to show that the pupillary reflex is not an all or none reaction. There are differences in pupillary reactions which are due to the development of the infant. These differences can be determined most accurately by using a lamp in which the intensity of illumination can be regulated and changed. The pupillary reactions of very young infants are difficult to examine. Much time is lost in arousing the infants so that the eyes may be observed. In some instances the eyes may be gently opened with satisfactory results; in other subjects the lids are swollen or the infants close their eyes so tightly that it is impossible to make a satisfactory examination.

Eye movements and coördinations can be determined only if the infant is completely awake. Care must be exercised in giving the stimulus to make sure that the light is not too strong. If a bright light is used the infant blinks and may even close the eyes or turn the head away. On the other hand, a weak light may be insufficient for a response. It was found that an illumination of about three foot-candles is sufficient stimulation for eliciting eye movements in most infants. The light was moved slowly from side to side directly in front of the infant's eyes. It is extremely important that the light be moved slowly since too rapid stimulation seems to give a stimulus of too short duration. The data, to be presented later, show that movements and coördination are the rule rather than the exception in newborn infants.

ALGOMETERS

Problems concerned with sensitivity to pain continue to entice psychologists into new investigations. There is no doubt that infants possess pain organs at birth but the degree to which these receptors are developed in the newborn child has never been fully explored. General observation has shown that some infants cry when they are pricked with a needle. Carefully controlled observation, on the other hand, demonstrated that some infants do not respond to a needle prick even though the stimulus be repeated several times. Such striking differences in infants' responses to pain stimuli make the problem fruitful as a field of research. Several types of instruments have been employed to elicit a response to pain but there is still much exploration needed in this aspect of infant development.

In order to make adequate measurements of responses to pain, it is obvious that some way must be found to stimulate the infant with measurable stimuli which can be changed in intensity. The literature contains many reports of the results of investigations in which pain stimuli were applied by a needle or pin. Many observers trusted their own ability to apply the stimulus with constant strength. Even superficial reflection upon such a procedure shows the inadequacy of such experimental conditions.

Figure 2 presents schematically one of the instruments devised for the application of quantatively controlled pain stimuli. A protective cap was constructed in such a manner that the position in which it was set determined the pressure which could be applied on the needle. The cap could be set in any one of eighteen positions. A coil spring served to give a uniform amount of pressure on the needle at any given stop. Preliminary experimentation revealed that the first three degrees were sufficient to elicit a response in most infants. It is probable that infants who did not respond to the strongest of the first three degrees of stimulation would have required enough pressure on the needle to break the skin.

In giving a pain stimulus the cap was set so that the needle could indent the skin only a given distance. The cap served to determine the intensity of the prick and also to guard the point of the needle against a possible movement of the infant's head or hands. The apparatus was held perpendicular to the point to be stimulated. A stimulus was given by pressing the instrument on the skin until the protecting cap touched at all points. If a first trial failed to produce a response a second stimulus was given to make sure that a nerve ending had been stimulated. A barely perceptible stimulus was designated as degree 1, a slightly stronger stimulus as degree 2. Points 1 to 9 were numbered on the instrument with dividing lines at half way points. Infants were not stimulated beyond degree 3 except in the preliminary stages when several stronger stimuli were used.

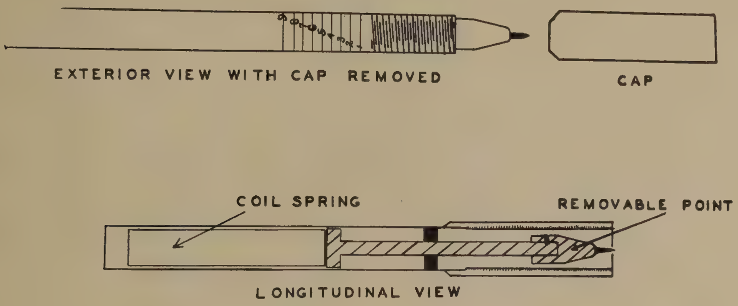

FIG. 2. SCHEMATIC DRAWING OF APPARATUS FOR PAIN STIMULI WITH NEEDLE

One problem of the present study was to determine the difference in the type of response elicited by a uniform stimulus applied on the leg and on the cheek. A very strong stimulus of constant intensity would probably produce a response regardless of the point stimulated. The limen of pain plays an important rôle in the character of the response elicited. If the stimulus is too weak nothing happens; if it is too strong differentiation of responses to stimuli on different parts of the body is impossible.

Time is an important factor in the interpretation of infant responses. It is quite common for a response to be delayed a few seconds. As we shall see later, the length of the latent period depends upon the strength of the stimulus and the responsiveness of the child. Observations showed that some infants made responses after a latent period of several seconds. Observation for only two or three seconds immediately after a given stimulus may lead to erroneous conclusions. Care must be exercised in applying the stimulus to avoid a summation effect. A variation of the procedure to insure a random order seems to be much more desirable than a set order of procedure. If the cheek were always stimulated first and the legs afterwards, for example, one might seem to get more activity to a stimulus on the legs if the latter stimulus followed immediately after that given on the cheek. Throughout the present study the first stimulus was given on the leg as frequently as on the face. Differences observed should therefore be a fair representation of characteristic responses.

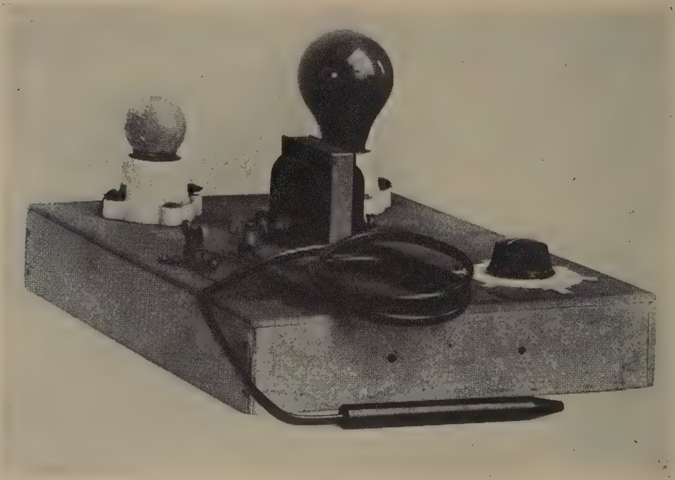

FIG. 3. PHOTOGRAPH OF APPARATUS FOR INDUCING ELECTRIC SHOCK

A response to a pain stimulus on one part of the body should have fully expended itself before a second stimulus is applied even to another member or segment of the body. The infant must be quiet before a stimulus can be given or repeated.

An algometer constructed according to the foregoing specifications is not wholly satisfactory for giving pain stimuli. The intensity of the stimulus can be regulated but the pain stimulus is complicated by the addition of pressure from the rim of the protective cap. It was found that some infants responded to a slight amount of pressure, but the response was neither as strong nor as persistent to a pressure stimulus as it was to pain.

To overcome this inherent weakness in the apparatus, an electrical algometer was developed. The first set-up included a dry cell, an induction coil, and an especially mounted electrode. Stimuli given with this electrical algometer revealed that a given intensity applied on the cheek and on the leg produced more sharply differentiated responses than were observed with the original apparatus. A dry cell, however, diminishes in strength with use. Thus some apparatus was needed which could be depended upon for a constant output of current. An electrical algometer[1] was obtained which produced stimuli varying from 0 to $12\frac{1}{2}$ milliamperes. Figure 3 is a photograph of the apparatus.

The experimenters selected a rheostat position at which the current was barely perceptible, then marked off four higher positions. It was found that some newborn infants responded to a stimulus which was lower than could be detected by the experimenters. A sixth position was therefore added to the original five steps. The amount of the transformed secondary current at the six rheostat positions was determined by placing an ammeter in the place of the electrode. The ammeter had a resistance of 250 ohms.

The electrode had a gap of approximately $\frac{3}{8}$ inch, which gave some resistance. It is impossible to give the exact amount of current received by a given subject since the skin resistance probably varies considerably from child to child. The transformer secondary current on six rheostat positions ranged from 0.34 to 0.83 milliamperes.

PRESSURE APPARATUS

An earlier study by Sherman and Sherman (33) showed that infants make defense movements in response to a pressure stimulus on the chin. Differences which exist in the reactions of infants to pressure stimuli can be determined and explained only by careful experimental procedures. It is impossible to estimate the exact amount of pressure applied unless quantified apparatus is used. It is likely that the experimenter who uses subjective techniques would unconsciously apply greater pressure on those infants who were the least reactive. An instrument was therefore devised which made it possible to give a pressure stimulus of a known intensity.

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[1] Through the kindness of Dr. David P. Boder, an electrical algometer was borrowed from Lewis Institute. Dr. Boder had constructed the apparatus for use in his experimental work.

Figure 4 presents a schematic drawing of the apparatus developed for this study. A small screw stop was placed in a plunger to limit its excursion and to serve as a marker in giving a stimulus. The degree of pressure applied was dependent upon the distance the plunger was pushed into the base of the instrument. The rounded knob on the protruding portion of the plunger was padded with cotton and covered by a chamois. A piece of sterilized gauze was placed over this part of the apparatus before stimulating a new subject. The instrument was calibrated in grams so that four different pressures could be given by holding the screw stop at any one of four points indicated along the slot.

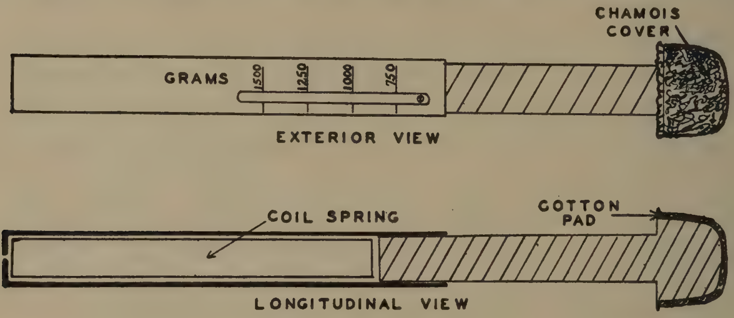

Fig. 4. Schematic Drawing of Apparatus for Applying Pressure Stimulus to Chin

Preliminary experimentation with the pressure apparatus revealed that a pressure of 750 grams was the most satisfactory position for producing reactions to the stimulus. If the pressure was weaker many infants failed to respond; if it was stronger a large number of infants responded with a general bodily reaction in which specific movements were difficult to differentiate.

The subject was placed on his back with the head held in mid-position by a nurse. The instrument was applied at an angle of approximately 30°. Pressure was applied for a period of thirty seconds. One experimenter counted the total number of arm movements, while the other counted defense movements of the arms and hands. A movement which touched the apparatus was considered a defense reaction. These defenses were of two types; movements of one hand to the apparatus or a coördinated movement of both hands. When an infant became aroused by the pressure and failed to free himself by arm or head movements other parts of the body were usually brought into action in an effort to remove the troublesome stimulus. Arching of the back was a common type of reaction but it usually followed other attempts to gain freedom. Records were kept of other types of responses, such as crying, arching of the back, kicking, squirming, and cessation of activity.

Caution must be observed to obtain comparable data. The subject's head must be held with a minimum of pressure. If the head is held with too great pressure, movements may be made to this stimulus rather than to the pressure on the chin. The nurse or assistant should grasp the infant's head as high as possible and permit as much freedom of movement as the experiment will allow. It is necessary, however, that the position be kept nearly enough constant that the apparatus may be accurately held in place.

MEASUREMENT OF LEG MOVEMENTS

Observation of the responses to a pressure stimulus revealed that some infants make pushing movements with the feet as pressure is applied to the chin. Several subjects were observed to push at the experimenter's hands with their feet. Such foot action seemed to be a part of the defense pattern of some infants. Motion pictures might have been used to record these movements, but a minimum of 500 frames would have been required for each subject. The expense involved ruled that technique out. It seemed desirable therefore to develop an apparatus for recording number of leg movements and at the same time measuring the strength of the movements.

The apparatus developed to measure number and strength of leg movements was so constructed that a kymograph record was obtained of the movements of each leg. The infant retaining apparatus is shown in figure 5. The board on which the infant lay was 9 inches by 30 inches with an adjustable head piece $4\frac{1}{2}$ inches high. The foot end of the board was divided by a partition 8 inches high and 12 inches long. This vertical partition of the apparatus served a dual purpose. It was necessary to provide a partition which would prevent the infants from rubbing the feet together as they kicked. This dividing board was also used to carry the cords over pulleys from the recording pens to the infant's legs. The subject's feet were tied by twilled tape to the cords which moved the two stylographic recording pens. Quilted pads were used to protect the infants from bruising themselves.

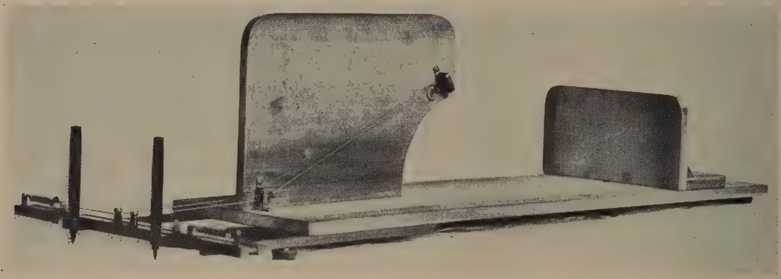

Fig. 5. Photograph of Retaining Apparatus for Infants in Recording Leg Movements

After placing the infant on the board in a dorsal position he was moved up to the dividing partition on the foot end of the apparatus with one leg on either side of the partition. The buttocks of the infant touched the end of the partition. The head piece was then brought up against the head so that the infant could not move longitudinally in either direction. The subject's legs were flexed approximating intra-uterine position and tied to the cords which led to the recording pens. A nurse held the infant's head gently to make sure that he did not squirm out of position. When everything was in readiness the kymograph was started and the record began. The kymograph was allowed to run a few seconds before the pressure was applied. A thirty-second record under stimulus conditions was then obtained.

The kymograph records showed the number of movements made by a subject in a given time interval. Since the kymograph revolved at a known speed it was possible to determine the number of movements in a given unit of time. The height of the reaction line indicated the strength of the kick. Strength of leg movements was measured in grams of pressure necessary to move the pen a given distance. A spring device held the pen in a zero position if no strength was exerted by the legs. The spring was carefully calibrated in terms of gram distance.

THE GRASP REFLEX

A number of investigators have reported that infants are able to support their body weight by grasping. Thus Watson, among others, published pictures of young infants apparently supporting themselves by grasping the experimenter's finger. The inference from a number of these reports seems to be that an infant's grasp reflex can be estimated in terms of his ability or inability to support his weight.

As we shall see later, numerous problems arise in the measurement and evaluation of the grasp reflex. A number of pertinent questions force themselves on the attention of the experimenter. How much do infants differ in strength of reflex grasp? Are there age differences? Are there differences between the two hands? When does the reflex diminish in strength? What effect does voluntary movement have on the reflex grasp? Is the strength of the reflex grasp related directly or inversely to handedness? The data assembled will be interpreted in the light of these problems.

A Chatillon Balance, spring cylindrical form, was adapted to measure the strength of the reflex grasp. This balance is graduated to 6000 grams in 50 gram divisions. Since each division is approximately 1 mm. long it is quite easy to read values to the nearest 25 grams. A schematic view of the balance as adapted for use is shown in figure 6. A small brass stirrup with a grasping surface $\frac{3}{16}$ inch in diameter by $1\frac{3}{4}$ inches in length was attached to the balance. A slide which exerted approximately 600 grams of tension was fitted into the slot of the balance. Any pull between 600 and 6600 grams could be registered by this device. The slide made it possible to read the performance after the spring had snapped back into position. It was therefore necessary to add 600 grams to the observed pull to obtain the actual value for each subject.

The strength of the reflex grasp was measured in the following manner. The infant was turned a few degrees to the side opposite the hand to be tested. The stirrup was placed in the infant's hand and the fingers closed. It was observed from the first that an infant had a greater grip or pull if the measurement was made just as the muscles began to contract. Contraction of the muscles was easily detected by the experimenter. As the muscles contracted the experimenter lifted the apparatus until the subject loosened his hold or until the total body weight had been lifted. While one experimenter lifted the infant the nurse and the second experimenter made sure that the subject was caught when the grasp was relaxed. Care was exercised to protect the

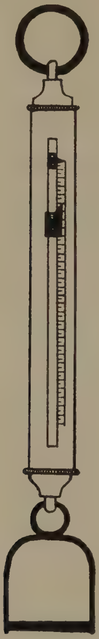

FIG. 6. SCHEMATIC DRAWING OF APPARATUS FOR MEASURING THE STRENGTH OF THE GRASP REFLEX

infant's face from a sudden jerk of the hand as the stirrup was released.

Repeated trials were made until the experimenters were certain that the infant had been given a fair chance to show the strength of his grasp. If the grasp slipped, if the apparatus were lifted just as the grasp released the stirrup, or if other conditions interfered with the test, a second or third trial was given. In some instances subjects failed to grasp after repeated trials. Such performances were recorded as refusals.

That there are wide individual differences in the reflex grasp will be shown by the data. Several precautions are suggested to those who may use this technique in other investigations. The state of the infant seems to have some effect on the strength of the grasp. The waking process, for example, apparently brings with it a series of muscular tensions and relaxations which make accurate measurements of the grasp reflex difficult. It appears as if the muscle-tone of the waking infant is often too poor for a strong grasp.

The speed with which the apparatus was pulled often affected the strength of the grasp. It was found that a slow, steady pull was the best means of obtaining the maximum strength of the reflex. A sudden pull often resulted in a sudden loosening of the hold. Infants were often unduly aroused by such a method, resulting in prolonged general activity and crying. It was also noted that forceful opening of an infant's fist to place the stirrup in its hand frequently resulted in arousing general muscular activity and crying, which interfered with proper measurement.

OTHER REFLEXES

Tests were made in the ordinary manner for a number of reflexes; the Achilles, patellar, plantar, Rossolimo and Brudzinski. When ankle clonus was discovered accidentally in several infants, seventy-five subjects were tested for this response. The plantar reflex was tested by pressure with a small brass rod, the stimulus being made by a pressure movement laterally from toe to heel. The infants were tested with light pressure, such as is ordinarily used in eliciting the plantar reflex, and also with heavy pressure.

OBSERVATIONAL RECORDS

It is difficult to make intelligent observations of the spontaneous activity of newborn infants, especially of characteristics which might be included within the term personality. And yet, nurses and other workers who are constantly in contact with newborn infants believe that the newborn often shows characteristics of personality sufficient for differentiation between one baby and another. Nurses report, for example, that some infants are characteristically amiable and contented, whereas others are irritable at the least provocation.

It was felt that more adequate records would be obtained by asking the nurses to check the presence or absence of given reactions when they observed the infants than if they were to make an interpretive report. Recording observations by checking was also found to be least time-consuming. The nurses checked their records quickly, and many expressed the belief that their recording was much more accurate than if they had been required to write a report on each infant.

Records were kept of an infant when it was bathed and dressed at 10 a.m., when it was taken for a feeding, and when rounds were made in the nursery. Every infant was also observed in the nursery at 7 a.m. before the activities of the day began. Whenever an infant was handled, a record was made of whether it was wet or dry and quiet or crying.

THE SUBJECTS

The infants ranged in age from several hours to sixteen days. The majority of the infants were less than ten days old. A total of 317 infants were examined of which 86 were reexamined. These infants were never reexamined, however, within a period less than twenty-four hours. Of the total number of cases, twenty-two were delivered by caesarean section, 53 were instrumentally delivered, and the remainder were delivered by the normal birth process.

CHAPTER II

REACTIONS OF THE EYES

PUPILLARY RESPONSES

The size of the pupils of eighty-three infants was observed. In estimating the size of the pupils, five categories were adopted, namely, small, moderately small, moderate, moderately large, and large. By preliminary observation and comparison of separate observations of the experimenters, a fairly constant agreement was reached regarding these classifications. Although no quantitative measure of size was made, differences in the size of the pupils were readily recognized. Furthermore, as was the case in other observations, an agreement of two experimenters making their observations independently was reached before an estimate was recorded.

The majority of the infants were awake when the size of the pupils was estimated, but a number were asleep. The results are shown in table 1. It is seen that when one does not take into account the sleeping or waking condition the per cent of large pupils is practically as great as the per cent of small. When infants are examined while awake, the pupils tend to be large, and when asleep, to be small. Lee (24) states that "in infants, the pupils are contracted; according to my observations, in from eighteen months to two years, they become more dilated." All the subjects of this study were under sixteen days of age, and yet approximately 43 per cent had moderately large or large pupils. It is probable that Lee's finding that the pupils become more dilated as the infant grows older is due to the fact that with advance in age the infant spends less time in sleep.

Lee also states that "sensory stimuli throughout the body produce dilatation by partly stimulating the ciliospinal center and by partly inhibiting the oculomotor center" and that "removal of the normal sensory impulses, as in sleep or hypnosis, produces a contracted pupil." Infants under sixteen days of age, however, spend most of their time in sleep and yet approximately 43 per cent have comparatively large pupils. According to our results, with one exception (classification moderate) the size of the pupils of infants who were asleep at the time of examination increased as the mean age decreased. Thus the mean age of the infants who had small pupils when asleep was 111.6 hours, moderately small, 64.2, moderately large, 30.6, and large, 6.6. The age factor must therefore be considered as significant as the sensory background in determining the size of the pupil.

TABLE 1

Size of pupils

SIZE	AWAKE			ASLEEP			TOTAL		
	Number	Per cent	Mean age	Number	Per cent	Mean age	Number	Per cent	Mean age
Small	11	19.6	61.8	12	44.4	111.6	23	27.7	88.2
Moderately small	6	10.7	94.8	5	18.5	64.2	11	13.2	71.0
Moderate	8	14.3	150.6	5	18.5	143.4	13	15.7	147.8
Moderately large	15	26.8	84.7	3	11.1	30.6	18	21.7	75.0
Large	16	28.6	100.2	2	7.5	6.6	18	21.7	90.6
Total	56	100.0		27	100.0		83	100.0	

Several infants were observed whose pupils were unequal. Such a condition must be considered exceptional.

REACTION OF PUPIL TO LIGHT

The reaction of the pupils of 273 infants to three intensities of light was tested. No record was obtained of the remaining cases, either because the infants' eyes were so swollen that they did not open (silver nitate reaction) or because the infants were crying or asleep. From table 2 it can be seen that for each strength of light used the mean age increased directly with the increase in adequacy of the response of the pupils. The adequacy of the pupillary response was measured in terms of the amount and speed of contraction. As stated in the discussion of the experimental conditions, the responses were classified as none, fair, and good, and at least two observers had to agree before an estimate was recorded.

As the stimulus increased in strength there was a decrease in the number of cases giving no response or only a fair response, and an increase in the number showing a good response. Also, with an increase in the age of the child, adequate responses were obtained with a decreased strength of stimulus. For example, the mean age of the infants giving a good response to a light of 12 c.p. was 110.5 hours, to 6 c.p., 121.1 hours, and to 3 c.p., 134.2 hours.

TABLE 2

Pupillary responses, both eyes—273 cases

AGE	STIMULUS								
	3 c.p.			6 c.p.			12 c.p.		
	None	Fair	Good	None	Fair	Good	None	Fair	Good
hours									
0.6– 24.5	30	28	4	11	30	25	3	26	48
24.6– 48.5	23	20	5	8	20	30	3	9	51
48.6– 72.5	13	29	9	2	16	31	0	3	51
72.6– 96.5	16	13	17	3	11	34	0	3	46
96.6–120.5	9	15	13	2	10	30	0	12	36
120.6–144.5	17	29	14	4	21	41	0	11	48
144.6–168.5	7	26	14	2	2	35	2	0	37
168.6–192.5	10	13	13	4	11	20	0	7	28
192.6–216.5	11	16	12	2	12	30	0	5	41
216.6–240.5	1	9	0	0	1	8	0	1	8
240.6–264.5	4	2	2	0	2	6	0	1	7
264.6–288.5	2	0	2	0	1	3	0	0	3
288.6–312.5	2	0	2	0	2	2	0	2	2
312.6–336.5	0	2	0	0	0	2	0	0	2
336.6–360.5	0	1	1	0	0	2	0	0	2
Total*.......	145	203	108	38	139	299	8	80	410
Mean age....	97.6	111.7	134.2	78.9	95.3	121.1	57.6	90.3	110.5

* Totals for the three intensities of stimulus are not the same because all infants were not tested with each stimulus.

Table 3 is a record of the minimum stimulus adequate for a good pupillary response, tabulated according to age in days. The mean age in hours decreased with the increase in intensity of the stimulus. For 3 candle power stimulus the mean age was 134.2 hours, for 6 candle power, 111.0 hours, and for 12 candle power, 82.2 hours. This is further evidence that the intensity of the stimulus is an important factor determining the adequacy of the resulting response, and also that the intensity of the stimulus necessary to produce similar responses may be decreased as age increases.

TABLE 3

Minimum stimulus for a good pupillary response, both eyes—209 cases

AGE	STIMULUS		
	3 c.p.	6 c.p.	12 c.p.
hours			
0.6– 24.5	4	21	23
24.6– 48.5	5	25	21
48.6– 72.5	9	22	20
72.6– 96.5	17	17	12
96.6–120.5	13	17	6
120.6–144.5	14	27	7
144.6–168.5	14	21	2
168.6–192.5	13	7	8
192.6–216.5	12	18	11
216.6–240.5	0	8	0
240.6–264.5	2	4	1
264.6–288.5	2	1	0
288.6–312.5	2	0	0
312.6–336.5	0	2	0
336.6–360.5	1	1	0
Total............	108	191	111
Mean age........	134.2	111.0	82.2

In a previous study, the stimulus was a small flash-light, just strong enough to produce a prompt response in the adult eye. The actual strength of the stimulus was unknown, but it was such that in most cases there was spasm of the lids when the light was thrown into the eyes. In the present study the strongest stimulus used (12 c.p.) produced blinking or closure of the eyes in only three cases. That the *strength* of the stimulus greatly influences the character of the response is evident in the discrepancy between our earlier findings and those of the present study. When the ordinary flash-light was used, the mean age of those giving no response was 1.8 hours, whereas the mean age giving no reaction to a 12 c.p. light was 57.6 hours, and to weaker strength of light, the mean age was larger. Mean age, however, is not descriptive of individual responses. Table 2, for example, shows that in 74 instances either a fair or good pupillary response was obtained between the ages of 0.6 and 24.5 hours, to a 12 c.p. light.

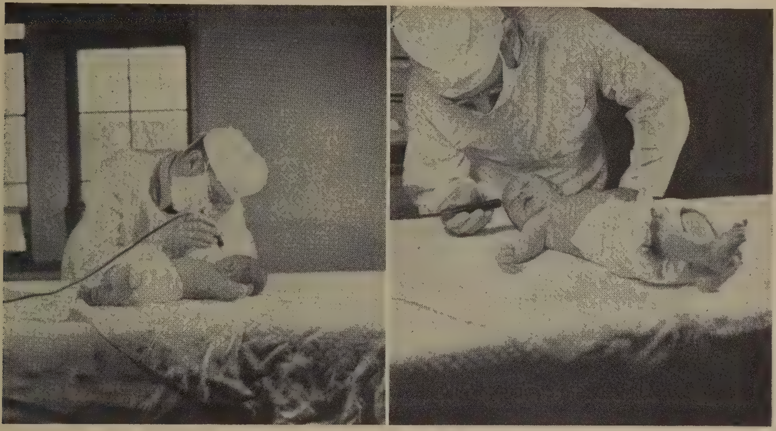

Fig. 7. Examination of Pupillary Reflex and Eye Movements

COÖRDINATION OF THE EYES

Records were made of the coördination of the movements of the eyes of 140 infants in response to a moving light. Eye movements of the remaining infants were not observed because they either fell asleep during the test, opened and closed their eyes persistently, cried, or were unable to open their eyes because of swelling.

The stimulus consisted of a circular spot of light variable in intensity, as previously described. The light was moved slowly in a horizontal direction about one foot in front of the infant's eyes. A total of twenty movements were counted. All the eye movements made were counted, not only those made in the direction of the stimulus, but also other eye movements, lateral, vertical and rotatory. The per cent of incoördination was then obtained by dividing the total number of incoördinated movements by twenty.

It is well known that newborn infants turn their eyes toward a moving light. Frequently, however, when a light is passed horizontally in front of them, they also turn their eyes in the direction opposite that of the movement of the light. They also frequently make vertical and rotatory movements. These vertical and rotatory movements may be seen as early as twelve hours. Occasionally one eye remains in a fixed position, especially that of inward deviation, while the other eye follows the light stimulus. This type of response indicates that a newborn infant may not make the same kind of pursuit movements that older subjects make.

TABLE 4

Examples of irregular eye movements

HOURS	
212	R. 1 error.* Moved eyes without regard to movement of the light
114	Made movements opposite from light. Also avoiding movements of head
12	R. 5 errors, (25%); L. 0. Eyes moved *up and down* and *rotatory* as well as laterally
166	R. 20 errors, (100%). Right eye did not move. Left moved laterally and rotatory
223	L. 6 errors, (30%). Left eye stood inward during six movements of right eye
2	R. No errors; L. 2 errors, (10%). Left eye stood still twice during movements of right
145	Appeared to "look at" objects
46	Internal strabismus

* The term error refers to incoördinated movements of the eyes.

Table 4 illustrates examples of irregular eye movement. The infants are identified in terms of their ages in hours. Attention is called to the cases in which one eye was fixed, while the other eye moved. In one case, as noted in the table, the right eye made 100 per cent error according to the method of recording, because it was fixed, while the left eye made twenty movements.

Concerning the ability of infants to make pursuit movements, McGinnis (25) states that ocular pursuit first appears during the third to fourth week. Before pursuit is established the majority of movements, however, occur in the direction of the movement of the stimulating object. Many of the movements are in the opposite direction. Ocular pursuit appears to develop with age.

TABLE 5

Eye movements—per cent of incoördination, both eyes

AGE	PER CENT									TOTAL CASES	MEAN
	0.0–4.9	5.0–9.9	10.0–14.9	15.0–19.9	20.0–24.9	25.0–29.9	30.0–34.9	35.0–39.9	40.0–44.9		
days											
0– 1	12	4	2		1	1	1			21	8.0
1– 2	6	3	3	1	2		1		2	18	14.2
2– 3	5	1	2	1	2		1			12	11.7
3– 4	5	5	2							12	6.3
4– 5	3	1	2	1						7	8.2
5– 6	11	5	1		1					18	5.6
6– 7	7	1	4							12	6.3
7– 8	6		4		1					11	8.0
8– 9	8	6	2	2				1		19	8.5
9–10	1	2	1				1			5	12.5
10–11	1	1								2	5.0
11–12				1						1	17.5
12–13			1							1	12.5
13–14											
14–15		1								1	7.5
0– 5	31	14	11	3	5	1	3		2	70	9.9
5–15	34	16	13	3	2		1	1		70	7.6
Total...	65	30	24	6	7	1	4	1	2	140	8.8

On the other hand, the data reported in a recent publication by Beasley (2) show that ocular pursuit movements occur within the first five days. The frequency of pursuit movements increases with an increase in the age of the subjects.

According to our results, newborn infants, even as young as two hours of age, make movements of their eyes in the direction of a light moved horizontally in front of their eyes. During the first few days of life, however, they also make many movements opposite to the direction of the stimulus. The purpose of this study, however, was not to determine when infants are able to make effective pursuit movements, but rather to observe their ability to make coördinated movements of the two eyes.

According to table 5, the mean per cent of incoördination of the infants under one day of age was 8.0, one to two days of age 14.2, and so on. Table 5 and figure 8 show that after a preliminary increase in the amount of incoördination on the second day the error decreased to a low value of 5.6 on the sixth day. Thereafter, the error increased to the tenth day, followed by a second abrupt decrease. The number of cases older than nine days was very small, however, and the data above this age are probably unreliable. There was, however, a very definite increase in the per cent of the incoördination from the fifth to the tenth day. No explanation can be offered at this time for this increase of incoördination. It should be noted, however, that at all ages

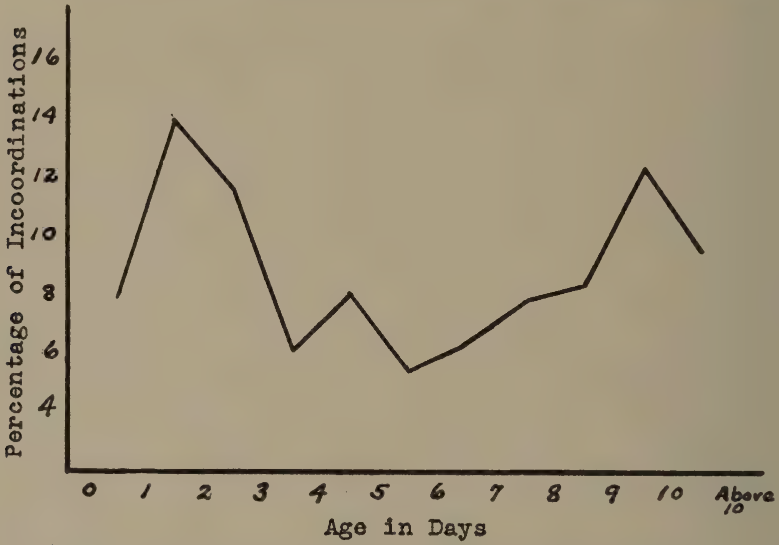

FIG. 8. PERCENTAGE OF INCOÖRDINATED EYE MOVEMENTS

coördination rather than incoördination was the rule. At no age was there a mean per cent of incoördination greater than 17.5, and the mean for the group as a whole was only 8.8. When the cases were divided into two age groups, the mean per cent of incoördinations for the younger group (0–5 days) was 9.9 compared to 7.6 for the older (5–15 days). These figures indicate that in general incoördination of the eyes decreases with age.

There were only slight variations in the mean per cent of error of the two eyes from day to day. The mean per cent of incoördination of the total group was 5.7 per cent for the left eye, and 5.6 per cent for the right eye.

It is difficult to interpret the significance of these eye reactions. Increase in adequacy of the pupillary reflex might perhaps be explained in terms of an increase in the anatomical adequacy of the stimulus-response pathways. This explanation is not entirely tenable, however, for histological studies have shown that the pathways are anatomically sufficiently developed for an adequate transmission of impulses. Another explanation for the increase in adequacy of an integral reflex such as the pupillary reflex is that functionally the pathways are not yet fully integrated. This functional integration takes place rapidly, and within a short time after birth the pupillary response becomes fully adequate in the sense that the pupils react as the pupils of adults.

The frequency of incoördinated eye movements in the infant and the fact that at times one eye is stationary while the other eye moves in lateral and rotatory directions also indicate that the integration of the type seen in a mature child is not yet fully developed in the newborn infant. These observations may have some significance for the theory of space perception. The final development of perfect coördination of the two eyes may be a factor of experience or learning (if we consider the results of experience as sometimes separate from learning). The probability that the development of space perception is partly a learning process is strengthened by observations of infants' developmental ability in manipulatory activities. Space perception and knowledge of space relationships apparently increase concomitantly with the increase in adequacy of general and specific sensori-motor processes. There seems, therefore, to be an interdependence between manipulatory processes and space perception, both increasing with age. From the adjustmental standpoint it is obvious that space perception is of relatively little importance to the newborn infant. His reactions are mostly immediate and to a great extent reflexive.

CHAPTER III

Responses to Pain Stimuli

Responses of infants to pain stimuli were studied in part to observe the reactions to pain-stimulating conditions and also to discover the types of responses which newborn infants make to a noxious stimulus of momentary duration. Ordinary noxious stimuli employed in experiments with infants are probably more complex than a stimulus of this type. A pressure stimulus applied to the chin, for example, the results of which will be discussed later, is difficult to analyze into its components. The response may in part be due to pain produced by the pressure although it is difficult to understand how the kind of stimulus employed could produce pain. Or, the important factor may be discomfort of the pressure itself which results in the defense reactions which infants make in response to pressure.

Although the term "pain" was applied in this study to both a needle stimulus and electric shock, it is not inferred that the two stimuli are similar. Both can be applied momentarily, however, and therefore can be controlled in duration better than other types of stimuli. Both can also be calibrated quantitatively, an important factor in any objective and quantitative study of infant behavior.

The character of the response of a large number of infants to a pain stimulus was observed. Table 6 is a list of the responses of infants to a pain stimulus (needle) applied to the face, arranged in order of frequency. The table shows that of the 287 responses 99 were stereotyped reactions characterized by bringing up the hand of the opposite side to the cheek, near the point stimulated. Many of these responses were also characterized by a pushing motion of the hand on the cheek near the site of the stimulated point. This response was typically elicited when the infant's head was placed in the lateral position before the stimulus was applied. The typical reaction then occurred as follows: If the head was turned to the right, and the stimulus was applied to the left cheek, the right hand was brought up to the point stimulated. When the head was turned to the left, and the right cheek stimulated, the left hand was brought up to the cheek. In a number of cases, the arm on the side stimulated was extended while the opposite hand was flexed toward the point stimulated. At times the head was turned further away from the direction of the stimu-

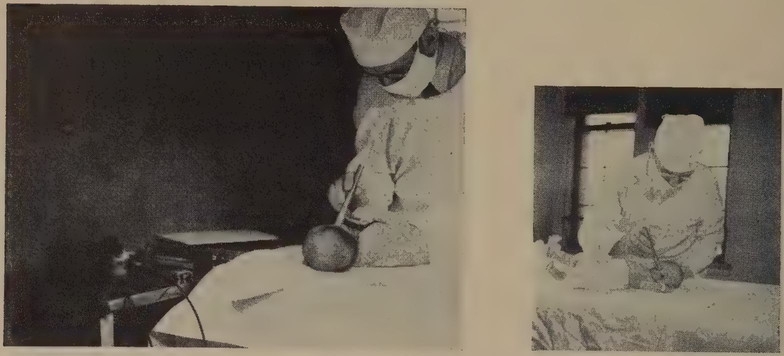

FIG. 9. TESTING FOR RESPONSE TO A PAIN STIMULUS (NEEDLE)

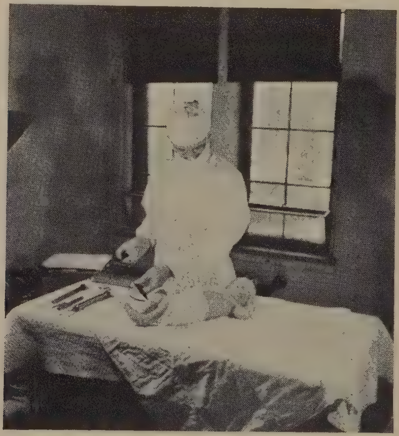

FIG. 10. APPLICATION OF ELECTRIC SHOCK STIMULUS

lus (14 cases) but in some instances the head was turned toward the side stimulated (9 cases). This type of reaction occurring so frequently and typically in a large number of infants may be regarded as a crossed flexion reflex, probably carried out at the brain stem level and mediated through the spinal fifth tract and the cervical cord segments. Although this typical response was usually unaccompanied by other activities, a number of varying types of behavior such as crying, arching of the back, extension of the head and startle, sometimes occurred at the time of the reaction.

TABLE 6

Responses of infants to pain stimulus (needle) on face

REACTION	FREQUENCY
Opposite hand to point stimulated	99
Startle	18
Crying	12
Startle, crying	8
Crying, moving limbs	7
Startle, moves limbs	6
Moves arms and then cries	5
Turns head, moves arms and cries	4
Turns head away, moves arms	4
Startle, cries, moves limbs	4
Turns head away	3
Moves hand on side stimulated to cheek	3
Startle, flexes limbs	2
Puckers mouth, moves limbs	2
Moves arms, legs and head	2
Moves arms, then turns head away and cries	2
Startle, moves limbs and head	2
Turns head away and cries	2
Raises hands and cries	2
Moves arms and then head	2
Miscellaneous	98
Total	287

The second most frequent response to the pain stimulus (needle) applied to the face was startle, and the third, crying. The frequency of these responses was, however, much less than that of the crossed flexion reflex described above.

Table 7 shows some of the characteristic responses of infants when the stimulus (needle) was applied to the leg. The most frequent response was flexion of the leg stimulated. Crying was not frequently observed in response to this pain stimulus. Crying can be elicited, however, as an accompaniment of almost every response, if the stimulus is sufficiently intense. It was observed that the intensity and suddenness with which a pain stimulus was applied determined in large measure the nature of the reaction. If the stimulus was applied with great intensity and very quickly, the response was quite generalized. When applied with the minimum intensity sufficient for a response, the reaction was usually localized. It was also observed that when the stimulus was applied for a relatively long time on the

TABLE 7

Responses of infants to pain stimulus (needle) on leg

REACTION	FREQUENCY
Flexes leg stimulated	58
Extends leg stimulated	20
Flexes both legs	19
Elevates leg from table	18
Flexes foot of leg stimulated	15
Moves toes on side stimulated	9
Elevates both legs from table	7
Flexes leg and cries	5
Cries	5
Flexes leg and foot	3
Flexes leg and extends opposite leg	3
Flexes legs, moves arms	3
Extends toes on side stimulated	3
Extends legs	2
Moves legs, cries	2
Flexes toes on side stimulated	2
Extends foot	2
Flexes legs, cries	2
Moves legs	2
Flexes legs; startle	2
Moves arms and legs	2
Miscellaneous	46
Total	230

lower part of the leg the opposite foot often was drawn towards the point stimulated, as if in defense.

As stated above, flexion of the leg on the side stimulated was the most frequent response to a pain stimulus (needle) applied to the leg. It is apparently the most economic and immediate form of defense, that is, removal of the noxious stimulus by withdrawal. In a number of cases when the stimulus was continuously applied as the infant flexed the leg, extension followed, accompanied by a drawing up of the opposite leg with pushing motions toward the stimulated point. Startle was observed in few cases, probably because the stimulus was relatively less effective when applied to the leg than to the face, and not sufficient to produce a reaction of the entire body.

When the stimulus applied to the face was a slight electric shock, the crossed reflex of the arms was observed in only eight of sixty-three responses. The typical reaction to electric shock was startle and crying. In three instances the arm opposite the side stimulated was elevated and moved upward, but the hand did not approach the point stimulated. An electrical stimulus is probably more diffuse than a needle prick and consequently there is a diffusion of response, which may account for the greater frequency of startle than of the crossed flexion reflex.

In a previous paper (33) it was shown that the head end of the infant is more responsive to a pain stimulus than the foot end. The number of needle pricks necessary to produce a response when applied to the cheek was less than that necessary to produce a response when applied to the leg.

In the present study two types of pain stimuli were employed, a needle and electric shock. The reactions of infants to both types of stimulation showed that there is a clear-cut difference in the amount of stimulation necessary to produce a reaction when the anterior and posterior portions of the body are stimulated. These differences are shown in tables 8 and 9. It can be seen that of 280 responses to a needle prick of intensity 1, 155, or more than half, of the responses occurred following stimulation of the face. Likewise, for each degree of stimulation, the number of responses was greater when the stimulus was applied to the face than to the leg. An exception was observed in the responses to stimulus intensity 2½ where, however, the number of cases was small. Only a small number were tested with the electrical apparatus. The response to this type of stimulus also showed that the face was much more responsive than the leg to identical strengths of stimulation.

When the responses were tabulated in terms of the minimum stimulus producing a response, the data again showed that the face is more reactive than the legs. By "minimum" stimulus is meant the smallest intensity of stimulation which resulted in a reaction, no matter how slight. The relationship between responsiveness to a minimum stimulus of face and leg is shown in tables 10 and 11.

TABLE 8

Responses of infants to a pain stimulus (needle)

	STIMULUS INTENSITY			
	1	1½	2	2½
Number of responses to leg	125	119	39	3
Number of responses to face	155	129	43	3
Total	280	248	82	6

TABLE 9

Responses of infants to a pain stimulus (electrical)

	STIMULUS INTENSITY			
	1	2	3	4
Number of responses to leg	8	7	2	1
Number of responses to face	33	23	8	2
Total	41	30	10	3

In table 10 it can be seen that of 280 responses to minimum stimulation with a needle stimulus of intensity 1, 155 were reactions to stimulation of the face and 125 of the leg. A similarly greater frequency of response to stimulation of the face is seen in the reactions to other stimulus intensities.

Table 11 shows the responses to minimum electrical stimuli. Although the number of responses observed was much smaller than to a needle, the greater reactivity to stimulation of head than leg was again seen.

On casual observation it was noted that the differentiation of head and leg end was somewhat less sharp in the older than the younger infants. This is probably due to the fact that as age increases, sensitivity differences become less clear cut. This does not mean that the cephalic end becomes less reactive, but that methods of stimulation ordinarily employed are probably less effective in demonstrating the differentiation.

TABLE 10

Responses of infants to minimum stimulus (needle)

	STIMULUS INTENSITY			
	1	1½	2	2½
Number of responses to leg	125	65	24	1
Number of responses to face	155	71	27	3
Total	280	136	51	4

TABLE 11

Responses of infants to minimum stimulus (electrical)

	STIMULUS INTENSITY			
	1	2	3	4
Number of responses to leg	8	6	0	1
Number of responses to face	33	19	3	0
Total	41	25	3	1

Irwin (19), in his study of four infants during the first ten days of life, found that the movements of the anterior region gained in dominance over the posterior as the ten day period advanced. Observations of animals, however, have shown that anterior dominance is present from the start. Coghill (quoted by Langworthy (23)) studying amblystoma, stated that "the first movements are made by the most anterior part of the muscle system of the trunk." Hartmann (16) observed beating of the forelegs but no movement of the rear legs in the seven-day-old opposum.

A number of observers are opposed to the view that the cephalic end of the newborn infant is more responsive than the caudal on the basis that general observations show more movements of the posterior than the anterior end. Close analysis indicates it is true that when a stimulus is sufficiently intense, in some cases intense enough to cause startle, many free movements are made by all the limbs, especially the legs. The criterion of reactivity, however, is not the number of movements, but the responsiveness to a minimum stimulus.

TABLE 12

Relation of age to response to a pain stimulus (needle)

	STIMULUS INTENSITY			
	1	1½	2	2½
	Mean age in hours			
Responses to leg	110.9	109.2	94.8	66.0
Responses to face	114.0	103.2	93.0	66.0

Table 12 shows the relation of age of the infant to the response to pain stimulation with a needle. It is seen that to stimulus 1, the mean age of response for the leg was 110.9 hours, for stimulus 1½, 109.2 hours, for stimulus 2, 94.8 hours, and for stimulus 2½, 66.0 hours. A similar decrease was observed in the intensity of stimulus necessary to produce a response as the age of the infant increased, when the stimulus was applied to the face. This might be expected from inferences from other studies in which it was found that the threshold for many responses decreases as the newborn infant grows older.

Analysis of the responses to the minimum needle stimulus applied to the face showed that the minimum stimulus which will produce a response must be stronger, the younger the infant.

The mean age in hours at which a minimum stimulus produced a response decreased directly with the increase in strength of the stimulus. Two hundred fifty-six infants were examined. The mean age for a response to a minimum stimulus 1 was 115.1 hours; to stimulus 1½, 98.2 hours; to stimulus 2, 88 hours; and to stimulus 2½, 66.6 hours.

Similar results were obtained for the responses to a needle stimulus applied to the leg. Two hundred fifteen infants were examined. The mean age for a response to a minimum stimulus 1 was 112.8 hours; to stimulus 1½, 103.3 hours; to stimulus 2, 92.1 hours.

From the reactions to a needle prick, it is clear that for this type of pain stimulus the threshhold for pain definitely and regularly decreases with advance in the age of the infant. While the results of this study on the response to pain stimuli corroborate the previous findings of the authors, the curve for reactivity was not found to be exactly the same. This may be due to the fact that the strength of the stimulus in the previous experiment was not known, and also because the experimental control was not as precise. In the previous study (33) it was found that the mean number of pain stimuli necessary to produce a reaction was less for the face than for the legs, up to the point when one stimulus was sufficient to produce a response when applied either to the face or legs. The age at which one stimulus produced a response was much higher when the leg was stimulated than the face. The age at which one application of the stimulus to the face produced a response was forty-one hours, and when applied to the legs, seventy-six hours. In the previous experiment an increase in intensity of stimulation was obtained by repetition. This is a difficult procedure because the rhythm of stimulation may be different in different cases, and also because the intensity of the stimulus might vary although the needle was controlled by a spring. It is known, however, that even with such a control, the suddenness with which the stimulus is applied influences the intensity of its effect.

It is extremely difficult to interpret a response to a pain stimulus. The problem of adult sensitivity to pain is quite different from that of the infant. In adults the psychological setting for the examination of pain sensitivity is complex, and interpretation and expectation influence the results. Perhaps the responses of infants to pain stimuli cannot be called "pain" responses, as their psychological nature is unknown. But it is probably more accurate to describe the response of infants than adults to a needle stimulus or an electric shock as pain. The variety of factors entering into the adult's response to a pain-producing stimulus are eliminated in the infant. It therefore can be safely assumed that the infant's response to a needle prick or electric shock is essentially a "pain" response provided the stimulus is quantitatively controlled. When such a stimulus, for example, is applied suddenly or with force, a startle effect or generally disorganized behavior often result. Such behavior, however, is not necessarily indicative of pain, for it is also observed when any form of stimulation is applied suddenly or with too great an intensity. When the quantitative aspects of the stimulus and the method of its application are controlled, useful data concerning the responsiveness of infants may be obtained.

INHIBITION OF THE SUCKING REFLEX BY PAIN

In five cases it was observed that sucking was not inhibited by a pain stimulus (needle). Four of these subjects made no response to the pain stimulus of the maximum degree employed. They continued sucking the fingers uninterruptedly, even when the stimulus was repeated. These observations are in accord with Baliassnikowa and Model (1), who reported that pain stimuli are ineffective in influencing the sucking response. In one infant, however, it was observed that sucking, though not inhibited by one degree of stimulus, was disturbed by a stronger stimulus. When the stronger stimulus was employed, the infant withdrew the finger from the mouth, cried and raised its hands above the head. This observation indicates clearly that before conclusions can be drawn regarding the inhibitory influence of pain stimuli, a number of factors must be carefully controlled, conditions which were mentioned previously. The character of the stimulus must be known. Its strength must be carefully controlled, and the site of stimulation must be described before interpretations can be made regarding the relationship between a given stimulus and the consequent response.

One infant, while sucking its fingers, was stimulated by a brief, weak, electric shock instead of a needle. When the stimulus was applied to the leg it was ineffective, but when applied to the face sucking stopped and the infant cried.

In two cases the following reaction was observed. When a pain stimulus was applied the infant began to draw his arms up to his face. It appeared that the hand accidentally touched the mouth. Thereupon the infant began to suck its hand and the general response to the pain stimulus ceased.

For various reasons it was impossible to study the inhibition of the sucking reflex of a large number of infants. The foregoing observations are included for whatever descriptive value they may have, but are naturally not convincing.

CHAPTER IV

DEFENSE REACTIONS

Some observers have stated that the activities of infants are not acquired by the typical learning process. McGraw (26), for example, states,

> In acquiring any new reaction pattern the infant experiences a degree of uncertainty or dyssynergia. A decrease in this dyssynergic aspect associated with a particular reaction pattern and an increase in the precision . . . of the performance is unquestionably a type of learning. Such learning is not, however, of the trial and error, or analysis and selection, variety. . . . Infants tend to make a partial response rather than a false one and "learning" consists of a completion of the reaction pattern rather than selection and elimination of responses.

According to our observations some infant activities are probably learned, that is, the process of their development is similar to that observed in the development of many later acquired activities which every one recognizes as a learning process. In following a light with the eyes, for example, the number of incoördinated movements definitely decreases as the infant grows older, and the number of accurate, well-coördinated movements increases. It perhaps can not be said that a definite selection of accurate movements takes place. Nevertheless, improvement does occur.

Various psychologists speak of "selection" as an integral phase of the learning of many activities. It is difficult, however, to describe the process of selection, and even more difficult to explain it. The term selection is obviously employed only as a description of the final process of the fixation of correct responses.

The difficulty involved in defining the learning process is apparent when the defense movements of infants in response to a pressure stimulus are analyzed. When pressure is applied to the face most young infants at first make random movements of the arms, associated with strong kicking motions of the feet and arching of the back. At times they strike at the stimulating object with one hand or the other, often with sufficient strength to push the instrument from the face. Less frequently, both hands are brought up to the instrument and make a pushing motion, with very definite combined coördination of the two hands. With advance in age the percentage of coördinated defenses increases and the number of so-called random movements decreases. It is difficult, indeed, to say confidently whether this process is a trial and error process, similar to that seen in the development of motor skills in older children. Granted that this is a method of selection of effective movements and the elimination of unsuccessful isolated movements, the learning process may still be somewhat different from that observed in older children. As we have seen previously, even the so-called pure reflexes increase in adequacy with increase in the age of the infant. In the case of increase in adequacy of such reflexes as the pupillary, it is difficult to describe the process as learning. But in the case of defense movements, the increase of adequacy with age appears to be a process in part similar to that of the trial and error variety.

Not all infants respond in the same manner to pressure applied to the face, although many react with thrashing movements of the arms, arching of the back, and pushing movements of the feet. Other infants merely lie motionless, arms outstretched. The responsive infants most often cry loudly and frequently continue their crying after the stimulus has been removed. This was observed both during the first ten days of life and later, up to about two months of age. It is not known what factors produce such behavior. It is probable however that one of the factors involved is a relatively low threshold of sensitivity to this type of stimulation which causes an overflow of impulses. This overflow leads to generalized behavior. This explanation is in part confirmed by the fact that a sudden strong stimulus produces the same type of reaction in most infants. The overflow effect was also observed in a number of cases when the infant began making strong movements of arching the back and kicking the legs, after attempts to remove the stimulus by defense movements of the hands were unsuccessful.

The occurrence of diffuse movements is probably associated with the diffusion of the nervous impulses and is observed in response to a number of types of stimuli. Sudden stimulation by pain, for example, results in the same sort of response as that which follows sudden stimulation with pressure. If the stimulus is continued, however, the response changes, particularly the reaction to pressure. If the stimulus, on the other hand, is brief, a latent period occurs during which few movements of the arms and legs are observed. When movements do begin, it is frequently observed that the intensity of the reaction increases with the length of time that the stimulus is held constant.

As we have seen previously, the nature and intensity of a response is determined in great part by the nature and intensity of the stimulus. Mention will also be made later of the fact that massive responses are probably due in great part to a diffusion of impulses. Irwin (19) maintains, however, that the behavior of the newborn infant can be analyzed into two general categories of specific movements and mass activity; the movements that involve the entire organism can be considered as mass activities, the specializations appearing later as reflexes and behavior patterns. It will be shown later that reflex and behavior patterns appear at the very same time that generalized activity appears and therefore cannot be classified as mere specializations. Carmichael (9) has shown that the mass activity of the newborn child is not of the type found in the early fetus but is rather the activation of groups of synergic muscles. The nervous system of the newborn infant is already structurally and functionally integrated for the appearance of very definite responses and definite reflex patterns.

Defense movements, as previously stated, were elicited by applying pressure to the chin. The infant was placed on its back and a nurse gently held the head in mid-position without applying greater pressure than was necessary to keep it in the mid-line. The stimulus, in the majority of cases of 750 grams intensity, was then applied. The pressure was continued for thirty seconds, and the number of movements made during this period was recorded.

The duration of thirty seconds was employed in part arbitrarily, and in part because this seemed to be the most favorable period. If the stimulus, for example, was held constant for a period of one and one-half minutes, some infants made intense diffusion movements and others became quiet and lay motionless.

TABLE 13

Per cent of coördinated defense movements of both hands to 750 grams pressure

AGE	PER CENT													TOTAL CASES	MEAN
	0	1–5	6–10	11–15	16–20	21–25	26–30	31–35	36–40	41–45	46–50	51–55	56–60		
days															
0–1	30		2		1								1	34	5.9
1–2	29	1	2											32	3.8
2–3	21	4	2											27	3.9
3–4	22		2	2										26	4.6
4–5	24		2											26	3.9
5–6	19	7	2			1								29	4.5
6–7	17	1	3	1				1						23	6.0
7–8	12		3	1			1							17	6.4
8–9	15	2	1	2	1			1						22	6.7
9–10	2		3	1										6	7.7
10–11	2				1									3	8.5
11–12	2				1									3	8.5
12–13	1				1	1								3	15.0
13–14	1													1	3.5
14–15			1											1	8.5
Total...	197	15	23	7	5	2	1	2					1	253	5.2

Table 13 and figure 11[2] show the increase from day to day in the mean per cent of combined coördinated defense movements of the hands, made in response to pressure on the chin. It is seen that infants make few combined coördinated defense movements of the two hands until the sixth day when an increase occurs.

Table 14 shows the distribution of defense movements of the right hand, according to age. Table 15 contains similar data for the left hand. The frequency of movements of the defense type of either the left or right hand was much greater than that of coördinated defense movements of both hands. It must be noted that a combined coördinated defense movement of both hands is a very complicated process.

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[2] The last two class intervals are omitted in the figure because each contained only one case.

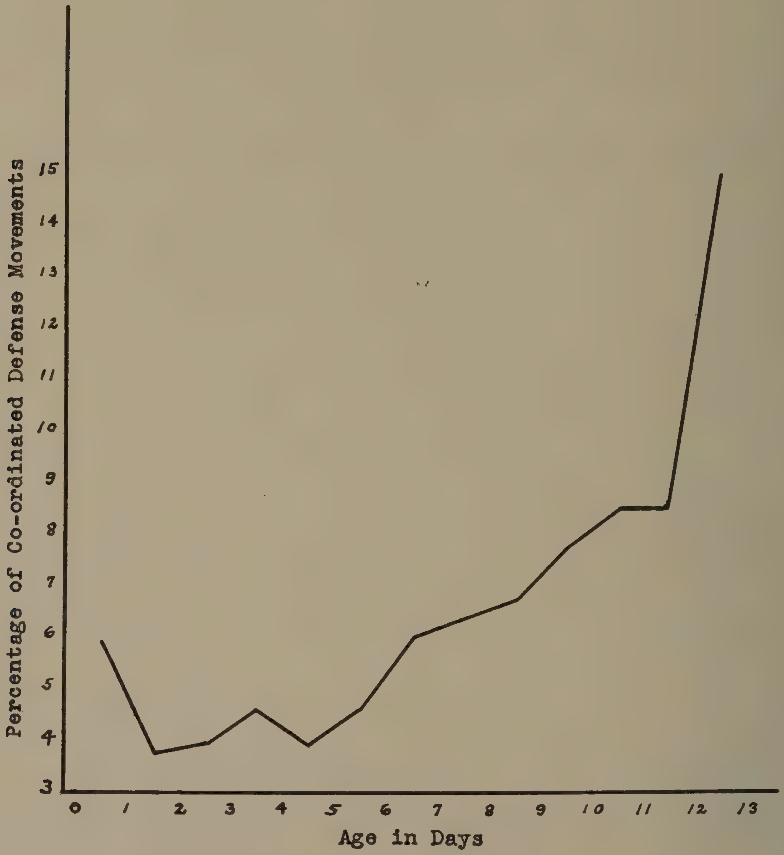

FIG. 11. PERCENTAGE OF COÖRDINATED DEFENSE MOVEMENTS OF THE ARMS, IN RESPONSE TO PRESSURE, ACCORDING TO AGE

With the exception of a number of irregularities, the percentage of defense reactions increased with increase in the age of the infant. Individual variations were frequent and the question

TABLE 14

Per cent of defense movements of the right hand to 750 grams pressure

AGE	0–10	11–20	21–30	31–40	41–50	51–60	61–70	71–80	81–90	TOTAL	MEAN
days											
0–1	21	2	6	2	1	1		1		34	16.6
1–2	21	5	4	2						32	11.9
2–3	15	4	6	1	1					27	14.5
3–4	14	8	2		2					26	13.7
4–5	11	7	2	1	3	1			1	26	21.0
5–6	7	5	9	5	2		1			29	23.9
6–7	13	4	5	1						23	13.4
7–8	5	4	3	3	2					17	21.9
8–9	5	6	4	2	2	1	2			22	30.6
9–10	1	3	1		1					6	21.0
10–11	1		2							3	19.3
11–12		1	1		1					3	29.3
12–13		1	1	1						3	26.0
13–14	1									1	6.0
14–15			1							1	26.0
Total...	115	50	47	18	15	3	3	1	1	253	18.1

TABLE 15

Per cent of defense movements of the left hand to 750 grams pressure

AGE	0–10	11–20	21–30	31–40	41–50	51–60	61–70	71–80	81–90	91–100	TOTAL	MEAN
days												
0–1	18	6	4	1	3			1		1	34	19.2
1–2	17	6	6	1				1		1	32	17.6
2–3	16	1	4	3	3						27	17.1
3–4	9	5	5	2	3	1			1		26	23.7
4–5	12	2	3	6	2		1				26	21.4
5–6	10	8	4	2	4	1					29	20.8
6–7	8	5	4	1	1	2	1	1			23	24.7
7–8	7	3	4	1	1		1				17	20.1
8–9	8	4	3	2	3		1			1	22	25.6
9–10	1	2	1		2						6	26.0
10–11	1			1	1						3	29.3
11–12	2					1					3	22.7
12–13			1	1		1					3	39.3
13–14			1								1	26.0
14–15	1										1	6.0
Total...	110	42	40	21	23	6	4	3	1	3	253	21.3

again arises whether the thirty seconds period of stimulation is the optimum period. In some cases it was observed that the adequacy of defense movements increased when the stimulus period was made longer. In other cases disorganized diffusion movements replaced coördinated movements when the stimulus was applied longer than thirty seconds. There was a variable latent period before specific movements were made, and in a number of cases before any kind of movement was made. Possibly this latent period influenced the proper evaluation of the infants' ability to make defense reactions since some, if not a large part, of the thirty seconds period elapsed before the infants reacted to the stimulus. Probably somewhat different results might have been obtained if the timing of the observation period had begun with the first movement.

During the defense reactions of the coördinated type, the palms of the hands were frequently opened when the infant made striking motions. This was seen in many cases when the infant pushed the instrument off the face. So-called aimless movements were in general made with closed fists, and during rest the majority of infants kept their hands closed. The opening of the palms is probably an aid to the defense function of many of the movements of the newborn infant.

Many of the infants' defense reactions to the pressure stimulus were strikingly accurate, the hands locating the stimulus at its very application to the chin. Sometimes an infant slashed at the offending object, making diffuse movements of the arms and hands before defense movements appeared. In general the infant at first made defense movements of the right or the left hand before a combined coördinated defense movement of both hands appeared. This indicates that even within the thirty seconds period of stimulation some type of selection of defense was made. It appeared that when unilateral movements were unsuccessful in removing the noxious stimulus, both hands were employed in a combined coördinated pushing movement of defense. It is possible, of course, that the percentage of coördinated defenses might have been greater if the stimulus had been continued for a longer period. In the few cases in which this was tried, however, the coördinated defenses decreased in frequency after a time and diffuse responses took their place. This was probably due to overstimulation and therefore resulted in a diffusion of impulses and hence a diffusion of responses.

In thirty-four cases the defense reactions were so accurate that the infant either grasped or pushed the instrument from the face. In a number of cases the infant pushed the instrument from the face two or three times during the observation period. One infant, 124 hours old, and one infant, 284 hours old, pushed the instrument off the face four times with the right hand during the observation period. In several cases the infants pushed the instrument off the face as soon as it was again placed in position, that is, the first defense movement following replacement of the instrument resulted in pushing the instrument away.

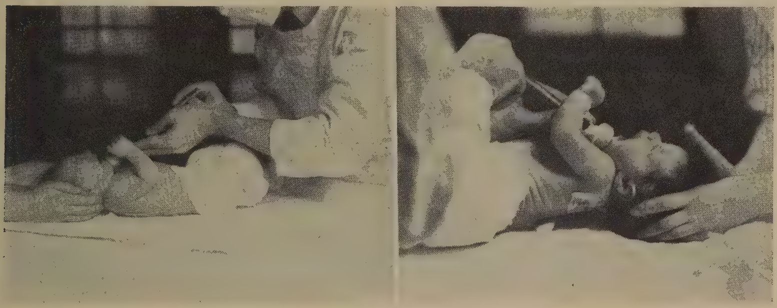

FIG. 12. APPLICATION OF PRESSURE STIMULUS

The accuracy of the movements of these infants was compared with that of the total group of infants. Table 16 shows this comparison. The data show that the infants who grasped or pushed the instrument from the face made a significantly greater number of arm movements than the total group. The percentages of their defense movements were also greater, the differences being considerable. This apparently indicates that an increase in number of arm movements results in an increase in the proportion of defense movements. Evidently these infants were more responsive than the group as a whole, and their precision in removing the instrument from the face may be related to this factor.

The data were also analyzed to discover whether the hand which characteristically pushed the instrument from the chin also made the most defense movements. The analysis showed that eighteen of twenty-seven infants made most defense movements with the hand which they characteristically employed for pushing the instrument from the face. Three infants made most defense movements with the opposite hand. Six infants pushed the instrument away an equal number of times with either hand.

The infants who grasped or pushed the instrument from the face were over 100 hours old, with five exceptions. These five infants were all above the age of fifty hours. It was also observed that only twelve of these infants cried during the period that the pressure stimulus was applied. As stated elsewhere, the infants who made diffuse and dispersed movements were the most likely to cry during the response period. Apparently crying is associated with a diffuse and, in a sense, disorganized type of reaction.

TABLE 16

Defense movements of infants who grasped or pushed instrument from face, compared with defenses of total group

	INFANTS PUSHING INSTRUMENT	TOTAL GROUP	*d*	P.E.$_d$
Average number of movements	16.0	13.0	3.0	0.572
Defenses, right hand	23.8%	18.1%	5.7	2.169
Defenses, left hand	27.3%	21.3%	6.0	2.321
Defenses, both hands	6.5%	5.2%	1.3	0.888

Thirty-two cases were observed in which the predominant reaction to the pressure stimulus was arching of the back. Slight arching of the back was an incidental feature in many cases, but in these thirty-two it was extreme, the infant supporting himself for a variable length of time upon the heels and occiput. This reaction was noted in response to a pressure of 750 grams, although in preliminary observations when a stimulus of greater intensity was used, even a higher percentage of infants arched the back excessively. Possibly these infants were more sensitive to the pressure stimulus and therefore reacted by a massive retreat, a type of reaction observed as a consequence of other forms of stimuli, when their intensity is great and their application sudden.

Table 17 shows the number of defense movements made by infants who arched the back, compared with the general group. It is seen that the average number of arm movements of these infants was 14.4 during the observation period of thirty seconds, whereas the average number of movements of the total group was 13.0, practically only one movement less. Yet the total group made a significantly greater per cent of combined defense movements and defense movements of the right hand. Apparently arching of the back is an avoiding mechanism of defense which when utilized interferes with the performance of more specific and effective modes of response. Obviously a massive muscular response such as arching of the back interferes with the effectiveness of a specific response such as a defense reaction with arm and hand. Although this type of response cannot be called a diffusion reaction, the result, so far as adequacy of defense is concerned, is about the same.

TABLE 17

Defense movements of infants who arched back, compared with defenses of total group

	INFANTS ARCHING BACK	TOTAL GROUP	d	P.E.$_d$
Average number of movements	14.4	13.0	1.4	1.049
Defenses, right hand	13.6%	18.1%	4.5	1.309
Defenses, left hand	19.3%	21.3%	2.0	1.685
Defenses, both hands	1.6%	5.2%	3.6	0.504

Infants often make pushing movements of the feet in response to a pressure stimulus applied to the face. In seventeen cases, pushing with the feet was so excessive that the records of these infants were analyzed for comparison with the total group. Many of these infants pushed forcibly against the arm of the examiner. Analysis of the arm movements of these infants is recorded in table 18. It is seen that the average number of movements and particularly the number of defense movements was smaller than for the total group. The per cent of combined coördinated defenses of both hands was only 0.3 in contrast to the percentage of 5.2 for the total group. The per cent of defenses of the right hand was 6.6 in contrast with 18.1 for the total group. The defenses of the left hand of these infants were not significantly fewer than those of the total group. The per cent of defense movements made by the left hand was strikingly greater than that by the right hand.

It is not difficult to explain the relative inadequacy of the arm and hand movements of these infants. The excessive energy employed in the pushing movements of the feet like that in arching of the back probably interferes with the adequacy of the movements of the arms and hands. Such interference is not peculiar to infants, for similar observations are common in the responses of older children and adults.

TABLE 18

Coördinated defenses of infants who pushed excessively with feet, compared with defenses of total group

	INFANTS USING FEET	TOTAL GROUP	d	P.E.$_d$
Average number of movements	11.3	13.0	2.0	0.835
Defenses, right hand	6.6%	18.1%	11.5	1.653
Defenses, left hand	17.0%	21.3%	4.3	2.553
Defenses, both hands	0.3%	5.2%	4.9	0.299

In describing the reactions to stroking the sole, it will be pointed out that among the variety of responses that occurred, there was frequently an extension of the leg on the side stimulated, and that often the opposite foot pushed at the point stimulated or touched the examiner's hand. Bryan, (4) too, observed that on stroking the heel, a "push-a-way" reaction was obtained from the free foot.

Regarding defense reactions of the arms, Shirley (34) observed that "when the doctor placed her stethoscope over the baby's heart, the baby . . . drew in the left arm in a rotary movement so that its wrist or hand frequently touched B's stethoscope or her hand. Reactions of this sort were noted in . . . 26.4 per cent of the 181 examinations."

In a number of cases, few if any movements of the arms and hands were observed in response to a pressure stimulus. In sixteen cases, no movements were observed, the infant lying quietly during the period of the application of the stimulus. In a number of other cases the infant ceased its movements after fifteen or twenty seconds of stimulation. These infants were all under fifty hours of age. The question arose as to whether these infants did not have some nervous system disorder, possibly a birth injury which interfered with their reactivity. In all but two of the cases, however, no clinical evidence was discovered which indicated a brain injury. This does not mean, however, that a brain injury did not exist, for the diagnosis of brain hemorrhage or injury, unless of the massive type, is difficult to make.

CHAPTER V

MOVEMENTS OF THE LEGS IN RESPONSE TO A PRESSURE STIMULUS

During the initial stages of this study of infant behavior it was observed that many leg movements occurred when a pressure stimulus was applied to the chin. In order to study these movements objectively and to discover the relationship between arm and leg movements in response to a pressure stimulus, records of leg movements of fifty infants were obtained. The movements were recorded on a kymograph by means of an apparatus previously described.

The records of four infants are illustrated in figures 13 and 14. The records were analyzed in the following manner. Each irregularity in the tracing was considered a pushing movement if it was large enough to equal a 200-gram pull on the recording pen. (In the reproductions of the four records each significant leg movement is represented by a numeral.) For ease of tabulation and analysis the extension and flexion of more than 200 grams strength were considered as two movements. In the records shown in figure 13 arrows have been inserted to show the occurrence of a coördinated defense movement of the arms. As will be seen later, strong movements of the legs were made more often when the arms and hands were moved coördinately in response to the pressure stimulus.

Twenty-two infants made the strongest forward leg movements with the leg opposite that of the dominant defense hand, whereas only seven infants made the strongest forward movement with the leg of the same side as the dominant defense hand. Only twenty-five of the fifty infants, however, had both leg and hand dominance. Regarding the number of movements, seventeen infants made more movements with the leg opposite the dominant defense hand and eight infants made more movements with the leg of the same side as the dominant defense hand.

Analysis was also made of the relationship between the leg and arm movements. The coefficient of correlation between the number of leg movements and the number of arm movements (omitting defenses) was 0.64 ± 0.06. The coefficient of correlation between the number of leg movements and the number of arm movements including defense reactions, was 0.57 ± 0.07. When the number of defense reactions alone were correlated with the number of leg movements, the coefficient was 0.41 ± 0.08. There are some indications therefore that with an increase in the number of defense reactions of the arms and hands, there is a decrease in the number of leg movements. The coefficient of correlation between age and number of leg movements was 0.26 ± 0.09. The correlation between the number of forward leg movements and the strength of the greatest forward movement of the right leg was 0.24 ± 0.09 and for the left leg, 0.34 ± 0.08. Seven of the fifty infants made no movements of the legs while the pressure stimulus was applied to the chin for the thirty seconds period. Of these infants four made no defense reactions of either arm, and of the remaining, only an occasional defense

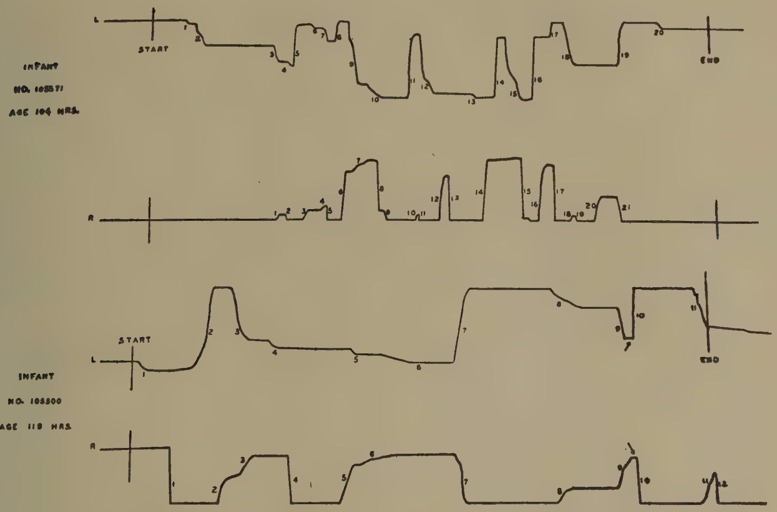

Fig. 13. Tracings of Leg Movements of Two Infants over 100 Hours of Age

reaction of one arm was observed and none of both. There was some evidence of a crossed reflex reaction between the arms and legs, that is, those infants whose dominant defense hand was on the right side made the strongest leg movements on the left side and those with the dominant defense hand on the left side made the strongest leg movements on the right side.

Table 19 presents a tabulation of arm and leg movements. The data were divided into three age groups, from birth to 99 hours, from 100 to 199 hours, and from 200 hours onward. The table shows that reactivity increased from the youngest to the middle group and then decreased in the oldest group. The average number of arm movements in response to a pressure stimulus was 6.0 for infants from birth to 99 hours, 14.6 for infants 100 to 199 hours old, and 8.3 for infants 200 hours of age and older. The average number of defense movements of the right and left hand, as well as the average number of coördinated defense movements also increased from the youngest to the middle group, and then decreased. Similar differences were found in

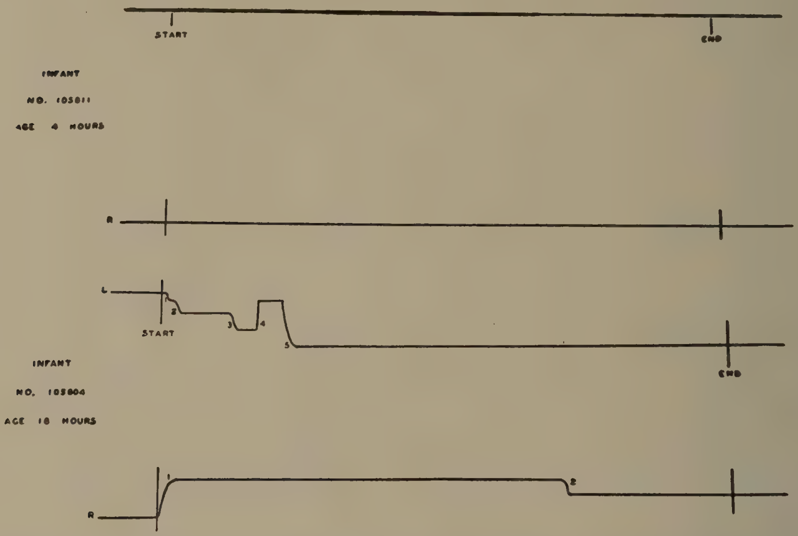

FIG. 14. TRACINGS OF LEG MOVEMENTS OF TWO INFANTS UNDER TWENTY-FOUR HOURS OF AGE

the number of significant movements of the legs. Thus the average number of significant leg movements of the right side was 3.4 for infants from birth to 99 hours, 7.7 for infants 100–199 hours old, and 6.8 for infants 200 hours of age and older. As the number of cases in the age group 200 hours and older was very small, no conclusion can be drawn from these data regarding the change in number of movements with advance in age. However, in the preceding section it was seen that defense movements increased with age, and presumably the number and strength of leg movements also increase as the infant grows older.

TABLE 19

Arm and leg responses of forty-nine infants to a pressure stimulus on the chin

RESPONSES	AGE GROUPS			ALL SUBJECTS
	0 to 99 hours	100 to 199 hours	200 hours and above	
Average number of arm movements	6.0	14.6	8.3	9.8
Number of defenses with right hand	0.7	3.9	2.0	2.2
Number of defenses with left hand	1.4	2.3	1.2	1.7
Number of combined coördinated defenses	0.1	0.5	0.2	0.3
Average number of significant leg movements—right side	3.4	7.7	6.8	5.6
Average number of significant leg movements—left side	4.3	7.5	5.7	5.8
Strongest leg movement—right side	326	430	413	378
Strongest leg movement—left side	357	523	444	434
Number of subjects	23	20	6	49

The data also show that the dominant defense hand of infants from zero to 99 hours old was the left and of infants over 100 hours of age the right. The term dominance is here defined on the basis of the average number of defense reactions made within the thirty seconds periods of observations. Similarly the average number of significant leg movements was greatest on the left side in the age group from birth to 99 hours and on the right side in the group 100 hours of age and older. When the movements were measured in terms of the strongest movement made by each infant during the thirty seconds period it is seen that the strongest movements occurred on the left side in all age groups.

Observations not recorded by the apparatus indicated that the movements of the legs had functions concomitant with the movements of the arms. Thus infants who responded to the pressure stimulus as though totally disorganized, for example by startle and failure to move the arms, also failed to move the legs. There seemed also to be a synchronization of the movements of the arms and legs. Thus the right arm and the left leg, and the left arm and the right leg seemed to be temporally synchronized. Analysis of the movements of the limbs of individual infants showed that when an infant made many random movements of the arms, the strength and number of significant leg movements was greater than when the infant made relatively few random movements of the arms. When the infant was successful in removing the noxious stimulus by pushing the instrument from the chin, the number of leg movements was significantly smaller than when the infant was unsuccessful. In general, therefore, the leg movements can be considered defense responses to the noxious stimulus employed in this study. They are concomitant aids to the defense movements of the arms made in the attempt to remove the stimulating condition. Infants who responded by massive retreat of the arms, that is, by arching of the back and flexion and extension of the arms, also made many strong movements with the legs.

CHAPTER VI

THE GRASP REFLEX

Various observers have measured the strength of the reflex grasp of the human infant, in terms of the length of time the infant is able to support his weight. Robinson (32), as early as 1891 stated that only two of his sixty cases were not able to support their weight for at least ten seconds during the first month of life. In contradistinction to this finding is Bryan's (5) statement that the majority of infants at birth can not support their weight by grasping. Observers also differ as to the duration of this reflex response. Hurlock (18) maintained that the reflex is distinctly weakened by the end of the first month and normally disappears completely by the fourth month. Freeman and Crosby (14) stated that reflex grasp disappears at one year.

In the newborn monkey, according to Richter (29), the grasp reflex is not strongest at birth but reaches its maximum from fifteen to forty days later. Of five animals studied by him the reflex was still present in one at the end of the 83rd day. It was equally strong in the two hands.

Involuntary forced grasping has been produced experimentally in animals and has been shown to occur in human adults as a manifestation of brain disease. Bieber and Fulton (3), for example, produced forced grasping in monkeys by destruction of premotor area 6. Freeman and Crosby (14) state that reflex grasping may result from focal brain lesions. These findings show clearly that reflex grasping occurs when given cortical areas which control voluntary movements are destroyed, with the consequent assumption of function by sub-cortical areas. It is probable, therefore, that the reflex grasp of the human infant may be due to incomplete functioning of specific cortical areas. As he matures, dominance is gradually taken over by the cortical areas, resulting in various behavior changes. That such changes in dominance take place is indicated strongly not only by the disappearance of the grasp reflex, but also by changes in other responses of infants. Experimenters have found, for example, that the grasp reflex disappears as voluntary behavior appears. In other words, as dominance shifts from the sub-cortical to the cortical areas, certain phases of behavior change from reflex to voluntary. Physiologically, of course, such a change is imperative. Adjustment would be impossible unless either the reflex or voluntary activity were dominant. Other data will be presented later as further evidence of this shift from sub-cortical to cortical dominance. The grasp reflex of the left hand of infants was observed to be slightly stronger than the right in many instances, although young children are predominantly right-handed. Cortical dominance is generally one-sided, that is, either the right or the left hemisphere is dominant. The lack of consistent and universal hand dominence in the newborn infant and the gradual development of right handedness in the majority of infants may be added proof of the gradual evolution of cortical dominance with localization of voluntary activity.

In the present study, the stirrup of the grasping apparatus was placed in one of the infant's palms as he lay supine. When he grasped the stirrup, a slight pull was made on it by the observer, the infant being permitted to pull downward as much as possible. If he failed to close the fingers spontaneously on the stirrup, the observer lightly pressed the fingers against the stirrup until he seized it firmly. He was then lifted gently until a maximum pull was obtained, immediately before the fingers released the apparatus. The strength of pull as indicated on the scale of the apparatus was then recorded and the procedure repeated with the opposite hand.

The strength of the reflex grasp of the right hand was measured in 268 cases, the left hand in 274 cases. Measures are not available in forty-nine cases for the right hand, and forty-three for the left, due to failure of the infants to grasp the instrument. Many of the infants who failed to grasp the apparatus either had just been fed, were asleep, or were crying. A small number of the infants who did respond were asleep at the time, however, and a much larger number were crying lustily. These conditions, therefore, can not be considered causes of inhibition of the reflex. A number of the infants who failed to respond to the first test were re-tested another day, but the number who failed on the re-test was about as great as the number who responded to the re-test. It can only be concluded, therefore, that some unknown factors were responsible for the inhibition of the reflex in those who failed to give a response.

Of the total number of infants whose strength of grasp was measured, twenty-seven (10.1 per cent) lifted themselves completely off the table with the right hand, and twenty-eight (10.2 per cent) with the left hand. Seven infants lifted the head from the table, but the majority did not elevate any part of the body. The youngest infant to lift the head and shoulders from the table with one hand was two hours old, and the youngest infant to lift himself completely from the table with one hand was nine hours old. The ability to do this was not closely related to age, for some infants at all of the age groups tested supported their entire weight with one hand. The average strength of grasp of those infants lifting themselves from the table with the right hand was 2862 grams, and with the left hand 2860 grams, compared to 1732 and 1765 grams, respectively, for the entire group of infants tested.

Figure 15 shows the average strength of grasp of each hand, according to age. The strength of the reflex increased irregularly from day to day. In order to discover, if possible, some indication of the onset of waning of the reflex, the records of a small number of older infants were also studied. These infants were examined in the out-patient department of the Bobs Roberts Hospital, but their records were not used in the general study because of the small number of cases and the wide age range (seventeen days to three months). Records are available of only seventeen older infants. The results, shown in figure 16, indicate that the grasp reflex begins to wane at about the eighth week. Even at the twelfth week, however, it had not yet decreased to

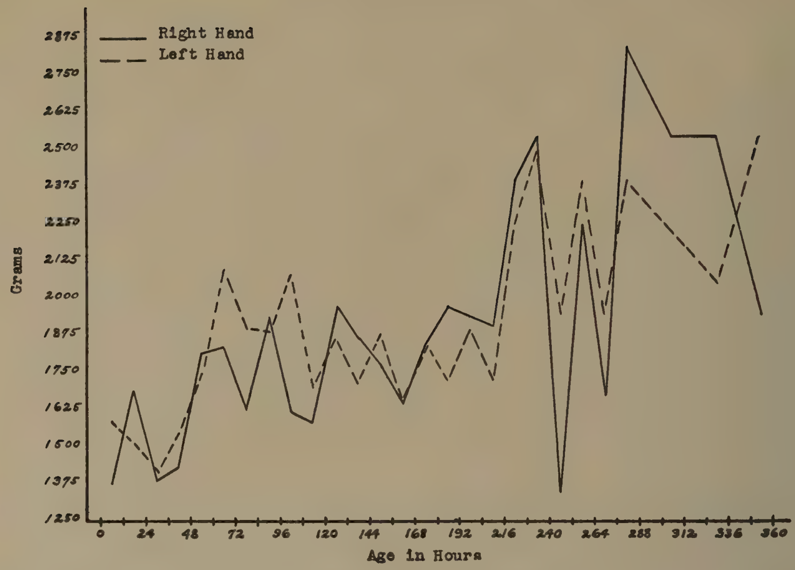

FIG. 15. MEAN STRENGTH OF THE GRASP REFLEX OF INFANTS, ACCORDING TO AGE

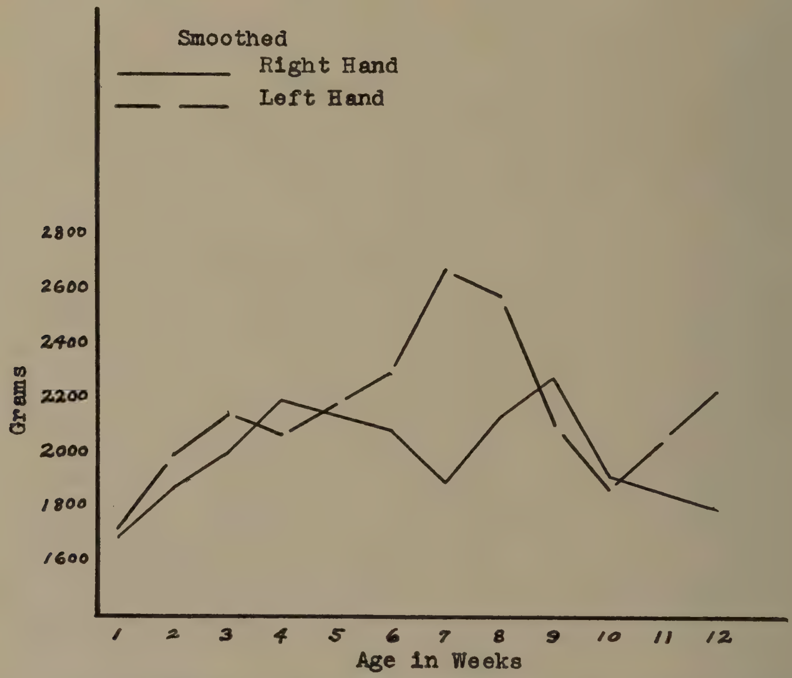

FIG. 16. MEAN STRENGTH OF THE GRASP REFLEX OF INFANTS, ACCORDING TO AGE

the level found during the first week of life, and no statement can therefore be made as to the time when the reflex disappears completely.

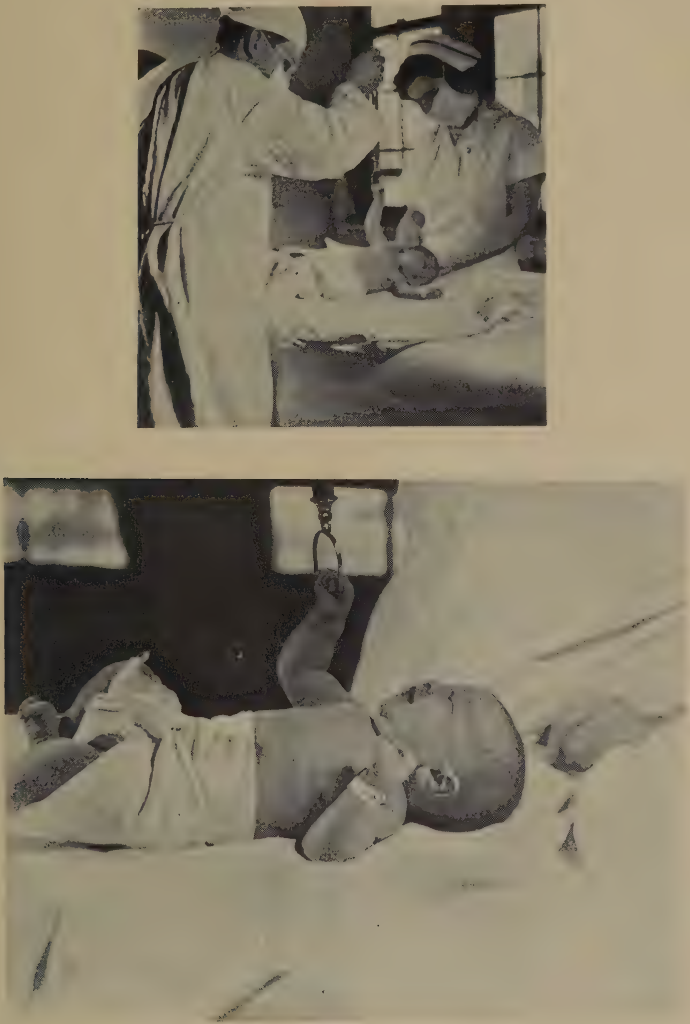

Fig. 17. Examination of the Grasp Reflex

Reference was made to the discrepancy in various observers' reports of the ability of newborn infants to support their weight by grasping. Dennis (12) has suggested that the reason for the disagreement may be due to the fact that those observers who declared infants *can* support their weight by grasping occasionally increased an infant's strength by causing him to cry. This suggestion is confirmed by the results of this study. The average strength of grasp of infants who cried when the reflex was tested was greater than the average for the group as a whole, comparing similar age groups. These results are shown in table 20. From the table it can be seen, for example, that the average strength of grasp of the one-day-old infants who cried while being tested was 1838 grams, whereas the average strength of grasp of the one-day-old infants in the entire group was 1621 grams. Likewise, the average strength of grasp of the right hand of infants who cried when tested was 2016 grams compared to 1733 grams for the entire group of corresponding age; corresponding figures for the left hand were 2105 grams compared with 1738 grams.

TABLE 20

Strength of grasp reflex of infants during crying

AGE	RIGHT HAND				LEFT HAND			
	Number of cases	Mean strength of grasp	Group mean	Number of cases	Number of cases	Mean strength of grasp	Group mean	Number of cases
days		*gm.*				*gm.*		
0–1	10	1,838	1,621	39	10	1,650	1,546	40
1–2	12	1,709	1,413	34	15	1,671	1,492	36
2–3	13	2,088	1,669	30	13	2,094	1,971	30
3–4	11	1,995	1,783	27	10	2,278	1,793	26
4–5	6	2,138	1,600	23	6	2,509	1,855	22
5–6	16	2,108	1,942	34	17	1,995	1,783	34
6–7	10	1,903	1,759	25	10	2,160	1,735	25
7–8	6	2,417	1,921	18	7	2,135	2,092	19
8–9	8	2,310	1,939	24	8	2,081	1,819	25
Total...	92	2,016	1,733	254	96	2,105	1,738	257

During sleep reflexes in general are diminished, and the grasp reflex is not an exception. Only eight infants were alseep when the reflex was tested, but in every instance except two the strength of grasp was less than the average of infants of corresponding age in the general group. These results appear in table 21.

In comparing the right and left hand, a number of differences were observed. The strength of grasp was equal in the two hands in only nineteen cases, all under ten days of age. In the majority of cases the difference tended to be small. A difference greater than 500 grams occurred only half as frequently as a difference less than this amount. The left hand had the advantage as a whole. The mean grasp of the left hand was 1765 grams, that of the right, 1732 grams. As shown in table 22, the left hand exceeded the right in 136 instances, the right exceeded the left in 121 instances.

No attempt was made to begin the test with one or the other hand. It is probable that the left hand was tested first as frequently as was the right. There is no possibility therefore of fatigue being a factor in the differences of the strength of the reflex. Neither is it probable that a warming-up effect was responsible for these differences.

It is not suggested that the differences are sufficiently significant to justify the assumption that infants are "left handed" in their reflexive responses. The data do show clearly, however, that in so far as reflex activity is concerned, right handedness does not exist in newborn infants.

The asymmetry observed in the grasp reflex is probably not significant except as it further emphasizes the possible superiority of the adequacy of the left side of the body in reflex adjustment to specific stimulating conditions, although some quantitative asymmetry was observed in other reflex reactions. From the standpoint of the immediate effect of the response, the grasp reflex is an important response for adjustment. As has been pointed out by many observers, this reflex is related to other righting responses and its occurrence and adequacy are important factors in the maintenance of the newborn infant. The inference is not made, however, that the adjustmental significance of this reflex is the same or even relatively the same as in infrahuman subjects. The adequacy of this response, in terms of its strength and frequency, decreases with the establishment of voluntary activity later on, partly because it later loses the function of maintenance of equilibrium and partly because it is incompatible

TABLE 21

Strength of grasp reflex of sleeping infants

AGE	RIGHT HAND			LEFT HAND		
	Number	Grasp	Group mean	Number	Grasp	Group mean
hours		*grams*			*grams*	
36.6– 48.5	1	800	1,430	1	400	1,553
72.6– 84.5	1	1,050	1,627	1	1,450	1,906
84.6– 96.5	1	1,325	1,930	1	1,450	1,882
96.6–108.5	2	1,483	1,618	2	2,160	2,083
132.6–144.5	1	480	1,870	0		
144.6–156.5	1	1,625	1,796	1	1,950	1,893
300.6–312.5	0			1	1,300	2,101
Total.......	7			7		

TABLE 22

Grasp reflex of right and left hands

AGE	LEFT AND RIGHT EQUAL	RIGHT EXCEEDS LEFT				LEFT EXCEEDS RIGHT			
		No test of left	Under 500 grams	Over 500 grams	Total	No test of right	Under 500 grams	Over 500 grams	Total
days									
0–1	2		14	7	21	1	8	8	17
1–2	3		10	4	14	2	11	6	19
2–3	3		7	3	10		12	5	17
3–4	2	1	5	5	11		10	4	14
4–5	2	1	5	2	8		5	8	13
5–6	3		13	6	19		11	1	12
6–7	2		7	4	11		8	4	12
7–8			4	4	8	1	8	2	11
8–9	1		12	2	14	1	6	3	10
9–10	1		2		2		2		2
10–11				1		1	3		4
11–12			1		2		1		1
12–13						1	1		2
13–14			1		1				
14–15								1	1
15–16						1			1
Total...	19	2	81	38	121	8	86	42	136

with voluntary activity in which choice is the important factor. The occurrence and disappearance of this reflex thus illustrates the progress from reflex to voluntary activity, concommitant with the establishment of anatomical and functional cortical integration. The grasp reflex in newborn infants may thus be considered as a pre-voluntary adjustmental reaction which gradually disappears as voluntary activities develop. The slight increase in the strength of the reflex with the increase in the age of the infant up to approximately the tenth day of age, is in part probably due to the same factors which are responsible for the increase in the adequacy of other reflexes and in part to the increasing strength of the infant. The factor of increasing strength is important in the interpretation of this response from the standpoint of this study, since the adequacy of the reflex was measured mainly in terms of the release of the hold on the apparatus at given strengths of pull.

TABLE 23

Fetal position at onset of labor, relation to strength of reflex grasp

POSITION	GRASP		NUMBER OF CASES
	Right	Left	
	grams	*grams*	
ODA	1,661	1,661	18
ODP	1,716	1,816	23
ODT	1,974	1,977	31
OLA	1,998	1,977	13
OLT	1,811	1,920	39
OLP	1,667	1,795	10

TABLE 24

Mean strength of grasp reflex of infants delivered by caesarian section or instrumentally, compared with group as a whole

	CAESARIAN		INSTRUMENTAL		TOTAL GROUP	
	Strength	Number of cases	Strength	Number of cases	Strength	Number of cases
	grams		*grams*		*grams*	
Right hand	1,853	33	1,842	73	1,732	268
Left hand	1,827	33	1,979	73	1,765	274

In the attempt to evaluate as large a number of factors as possible, as they influence the strength of the grasp reflex, the average strength of the grasp was computed for the infants and compared to their uterine position, immediately before delivery. Table 23 shows the relationship between the strength of the reflex grasp and the fetal position at onset of labor.

No attempt is made to evaluate this relationship from the standpoint of cause and effect. It is of interest, however, that the reflex grasp of the left hand was stronger than the right, regardless of fetal position before delivery (except for position OLA). It is obvious, however, that no conclusions or inferences can be drawn, because one cannot be sure that the fetal position immediately before birth is a criterion of the predominant intrauterine position before birth.

Richter (30) states that he found no relation between strength of the grasp reflex and the type of birth except that his two longest hanging records (grasp was measured in terms of length of time grasp was maintained) belonged to infants delivered through caesarian section. According to our records, the mean strength of the grasp reflex of infants delivered either instrumentally or by caesarian section was greater than that of the group as a whole. Table 24 shows the mean strength of the grasp reflex of infants delivered by caesarian section and by instrument, and the strength of the reflex of the total group.

CHAPTER VII

Miscellaneous Reflex Responses

The deep and superficial reflexes of a number of infants were tested. The results in general were similar to those of other observers, except for a variation in the percentage of positive responses. De Angelis (11) found the patellar reflex normal in 20.4 per cent, exaggerated in 54.5 per cent, much exaggerated in 21.6 per cent, absent in 3.5 per cent, and absent on one side in 5.5 per cent of eighty-eight newborn infants during the first week of life. Burr (7) states this reflex was present in sixty-one of sixty-six infants ranging in age from one hour to ninety days. Chaney and McGraw (8) examined twenty-five infants immediately after delivery (partunates) and 100 nursery infants (neonates) age 2–235 hours. The patellar was present in 68.7 per cent of the latter and 72 per cent of the former group.

The Achilles reflex was present in twenty-two of fifty-two of Burr's (7) cases, and Chaney and McGraw reported it present in 72.6 per cent of neonates and eighty per cent of partunates.

According to our results, the patellar reflex was present in 88.9 per cent bilaterally, and the Achilles reflex in 44.4 per cent (24.4 per cent bilateral; 20.0 per cent unilateral). The different percentages found by various observers are no doubt due to the method employed in eliciting the response. In this study, the maximum number of stimuli given was five, and if the response was not then elicited, it was recorded as absent.

After ankle clonus was accidentally discovered in one infant, seventy-five infants were tested for this response. Ankle clonus was found in 50.7 per cent of these infants (34.7 per cent bilateral; 16.0 per cent unilateral). The clonus in all cases was unsustained.

The occurrence of ankle clonus in over 50 per cent of the cases is of great significance for the interpretation of the functional nervous activity involved in the behavior of the infant. In the mature individual ankle clonus is a definite sign of irritability of the pyramidal tract system. This is in most cases concommitant with some destructive process in the upper motor neuron involving the pyramidal tracts. In the infant the occurrence of the ankle clonus shows that the pyramidal tracts are not intact functionally. As a later discussion will show, it is probably further evidence for the assumption that although the nervous system is intact from the standpoint of its gross structure, the cortical elements involved are not as yet integrated. The result is reflexive behavior of the type observed in adults when the upper motor neuron is disturbed.

The Rossolimo sign was sought in forty cases and elicited in 72.5 per cent (55 per cent bilateral; 17.5 per cent unilateral) of the infants. The occurrence of the Rossolimo sign in such a large percentage of cases is further proof of the high threshold of the nervous system in the newborn infant. Its presence is of the same significance as the presence of the ankle clonus, and perhaps also as of the presence of the positive Babinski reflex.

The Brudzinski sign was found in only two infants of forty tested (5 per cent). This is in conformity with the report of Schaltenbrand [quoted by Chaney and McGraw (8)] who stated that this reflex is rare in normal infants, but that he found it in about 10 per cent of young infants, in connection with the labyrinthine righting reflex of the head.

No relation of any of these responses to age was apparent, as they occurred in infants under twelve hours old as frequently as in older infants.

The literature is replete with reports of observations of the plantar reflex. It therefore seems unprofitable merely to add further observations. During our investigation, however, data concerning the rôle of the observer and the strength of the stimulus were obtained, and for these reasons a brief report is presented.

Many studies of the plantar reflex of infants have produced conflicting results. Different investigators have reported, for example, various results regarding the frequency of a positive Babinski sign in infants. Feldman (13) found that 67 per cent of children in their first year give a negative response (plantar flexion) and De Angelis reported that 43 per cent show positive responses. As various investigators have stated, the conflicting results of numerous observers are probably partly due to the large number of variables influencing the plantar response. One such variable, for example, is the sleeping versus the waking state. Waggoner and Ferguson (38) stated that there may be a reversal of the type of reaction to the same stimulus when the subject passes from the sleeping to the waking state. Bryan (4) found a difference in the age at which the Babinski sign can be elicited in the child awake and in the child asleep. Among other factors influencing the response are the degree of relaxation of the legs, whether the legs are quiet or in motion, whether the toes are flexed or extended when the sole is stroked, the location and direction of the stroke, the speed and intensity of the stimulus, and so on.

Since both the method and the conditions under which the plantar response is elicited influence the results, the reflex was tested under definite circumstances. The infants were tested only when awake; the leg was held lightly in one hand, slightly flexed at the knee. When the leg was relaxed, the stimulus was applied to the lateral surface of the sole, the stroke being made from the toes toward the heel. Two examiners made the tests; one tested 117 infants, using a single stimulus, the other, 163 different infants using two strengths of stimulus. When two types of stimuli were used the first was a light stroke. After the infant returned to a resting state, a second stronger stimulus was given. All stimuli were applied only when the toes were quiet and in mid-position, that is, neither flexed nor extended. Records were not made of 37 infants because they were restless or crying, constantly flexing and extending the toes, holding the toes in a position of extension, or making pushing motions with the legs when the examiner attempted to make the test.

In general the findings were similar to those previously reported by the authors. A number of observations made during the tests, however, showed that the nature and interpretation of the movements of the toes in response to stimulation are not simple. Any stimulus, for example a light touch on leg or thigh frequently produced extension of the toes. A positive Babinski sign was often obtained by pinching the abdomen or any other part of the body, especially the lower part. Stroking the leg gently also frequently resulted in extension and fanning of the toes. Only rarely was there flexion of the toes in response to such stimulation. Extension of the toes appeared to be at least in part a defense reaction, even though not accompanied by a flexion and withdrawal of the leg, a reaction which was very frequently observed. Any noxious stimulus produces a reflex response. This was observed, for example, when deep pressure was applied to the sole. In many cases the infant made pushing motions with the free leg against the stimulated foot. Whenever the leg was flexed in response to any type of stimulation the toes were likely to fan. Often plantar flexion then followed immediately. It was also observed that when the leg was flexed it was replaced on the table very slowly. At times plantar flexion of the foot was followed by a quick flexion of the opposite leg, the opposite foot then making downward pushing motions directed midway between the foot and the knee of the side stimulated.

The summation effect of stimuli, previously reported, was again observed; when repeated stimuli were applied to the sole of the foot flexion of the toes was the typical response. The summation effect probably overcomes the high threshold of the pyramidal tract system, resulting in the flexion response ordinarily obtained when the tract is intact structurally and functionally. This result offers additional basis for the belief that the pyramidal tract system is structurally sufficiently developed at birth for the transmission of impulses, but is functionally not completely integrated.

Table 25 shows the responses to stimulation of the soles of the feet of 117 infants. All of these tests were made by one examiner. In these cases, the stimulus was applied only once.

According to table 25 the positive Babinski sign occurred only to the extent of 15 per cent, whereas flexion of the toes was the most frequently observed response (38 per cent).

The rôle of the examiner in the interpretation of the plantar response is clearly seen when table 25 is compared with table 26.

The results shown in table 25 were obtained by a different examiner. The one examiner included under the heading of "positive Babinski sign" instances of extension of all the toes (so-called first phase) and extension of the great toe with fanning of the small

TABLE 25

Response to stimulation of soles of feet, 117 cases—all ages, one stimulus

RESPONSE	NUMBER	PER CENT
Flexion of toes	89	38.0
Positive Babinski*	35	15.0
Withdrawal of foot	24	10.3
Fanning	23	9.8
Flexion, extension of toes	15	6.4
Fanning, flexion of toes	15	6.4
Flexion, fanning	12	5.1
Extension, flexion of toes	11	4.7
Miscellaneous	7	3.0
Not recorded	3	1.3
Total	234	100.0

* Includes extension of all toes and extension of great toe with fanning of small toes.

TABLE 26

Response to stimulation of soles of feet, weak and strong stimuli—163 cases—all ages

RESPONSE	WEAK STIMULUS		STRONG STIMULUS	
	Number	Per Cent	Number	Per Cent
Extension of toes	98	30.1	92	28.2
Flexion of toes	89	27.3	106	32.5
Withdrawal of foot	27	8.3	22	6.7
Extension great toe, fanning	24	7.4	24	7.4
No response	24	7.4	8	2.5
Extension, flexion of toes	20	6.1	27	8.3
Extension of great toe	20	6.1	11	3.4
Miscellaneous	19	5.8	16	4.9
Fanning	3	0.9	6	1.8
Flexion, extension of toes	2	0.6	6	1.8
Flexion of foot	0	0.0	8	2.5
Total	326	100.0	326	100.0

toes (so-called second phase). The frequency of this response was 15 per cent. The other examiner recorded separately extension of the toes, extension of the great toe and extension of the great toe with fanning. The latter two reactions, according to table 26, occurred with a combined frequency of 13.5 per cent when the stimulus was weak, and 10.8 per cent when it was strong. If extension of the toes had been recorded as a positive Babinski sign, the respective combined frequencies of this response would have been 43.6 per cent and 39.0 per cent. Incidentally, these figures are very similar to the frequency of the positive Babinski sign (42.7 per cent) reported by the authors in a previous study (33). It seems likely that the discrepancy in the results of various investigators as to the frequency of the Babinski sign in infants is in large part due to the type of response regarded as a typical Babinski sign.

Table 26 shows that when the stimulus was weak, 30.1 per cent of the responses were extension of the toes and 27.3 per cent were flexion, an insignificant difference. When the stimulus was strong, the number of flexion responses increased and exceeded extension (32.5 per cent and 28.2 per cent respectively). Waggoner and Ferguson (38) found that in infants one to three days old a light stimulus resulted predominantly in extension and that a heavier stimulus resulted in an increase in the flexion response, although the latter did not exceed extension. Richards and Irwin,[3] however, in an excellent and detailed study of the plantar response of infants, concluded that "no differences between pressures for any type of response were significant." The increase in frequency of the flexion response when the stimulus is strong possibly is due to a threshold effect, being comparable to a summation of weak stimuli, which also produces a change from extension to flexion, as mentioned above.

An outstanding observation of the response to stimulation of the plantar surface of the feet was the wide variety of reactions. In tables 25 and 26 the responses were listed according to their chief characteristics. A single response without suppementary activity rarely occurred, however. For example, 44 of the 326 responses to a weak stimulus, and 69 of the 326 responses to a strong stimulus, listed in table 26, were complicated in various ways. Often the initial response was followed by a different

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[3] T. W. Richards and O. C. Irwin, Plantar responses of infants and young children: an examination of the literature and reports of new experiments. University of Iowa Studies in Child Welfare, 1935, XI, No. 1, p. 102.

TABLE 27

Variations of response to plantar stimulation

REACTION	STIMULUS		
	Weak	Strong	Total
Flexion of toes plus withdrawal of foot	5	12	17
Extension great toe, fanning, withdrawal of foot	5	9	14
Flexion of foot	5	8	13
Extension of toes plus withdrawal of foot	6	7	13
Flexion of small toes	4	2	6
Fanning plus flexion of foot	2	3	5
Extension great toe plus withdrawal of foot	3	1	4
Positive, negative plus withdrawal of foot	0	3	3
Withdrawal of foot, abduction of great toe	2	2	4
Flexion great toe, fanning small toes	2	2	4
Extension small toes	1	2	3
Extension, flexion of great toe	2	1	3
Flexion of toes plus extension opposite leg	1	2	3
Extension and fanning of small toes	1	2	3
Extension, flexion plus "pushing" at examiner's hand with opposite foot	0	2	2
Withdrawal of foot, flexion small toes	0	2	2
Flexion plus "pushing" at examiner's hand with opposite foot	1	0	1
Extension small toes, withdrawal of foot	1	1	2
Extension small toes, flexion great toe	1	1	2
Extension, flexion great toe, withdrawal of foot	0	1	1
Extension 2d and 3d toes, fanning between	0	1	1
Flexion great toe	0	1	1
Fanning, extension small toes, flexion great toe	0	1	1
Extension plus "pushing" at examiner's hand with opposite foot	1	0	1
Flexion great toe, withdrawal of foot	0	1	1
Extension great toe, fanning between 2d and 3d toes	0	1	1
Extension, flexion plus extension opposite leg	1	0	1
Flexion and extension of great toe	0	1	1
Total	44	69	113

kind of reaction. Also, two responses frequently occurred together. These variations are listed in table 27. The most common combined response was flexion of the toes plus withdrawal of the foot. Extension of the great toe, fanning and withdrawal of the foot was next in frequency. Flexion of the foot also was a common reaction. These withdrawal responses seem to be clearly of the defense type, observed also in the young of lower mammals, and organisms such as amblystoma. Coghill (quoted by Langworthy), for example, observed that the first reaction of amblystoma has the qualities of an avoiding reaction. Thus, a stimulus applied to the body produces a strong reaction of the muscles of the opposite side, carrying the organism away from the stimulating point. Also, according to Langworthy (23) stimulation of the foot-pad of one hind leg of the kitten produces withdrawal of that leg and withdrawal of both hind legs if the stimulus is of considerable intensity. Bryan, in eliciting the Babinski responses incidentally noticed that in stroking the heel, a "pushing-away" reaction was obtained from the free foot. This type of response was also observed when other stimuli were applied. As we have seen, a pressure stimulus applied to the face produces definite pushing motions of the legs, often of a rhythmic type.

As was mentioned previously, the large number of variations which occur in response to plantar stimulation must be analyzed partly in terms of defense reactions. More accessory movements occur following a strong than a weak stimulus, particularly movements of a withdrawal type. It is possible that even the typical Babinski response as it occurs in infants should be considered a defense reaction if it is accompanied by other types of responses.

CHAPTER VIII

INFANT BEHAVIOR PATTERNS

OBSERVATIONS OF NURSES

When plans were made for this study of infant behavior, the program included experimental observations of the personality reactions of newborn infants. When an attempt was made to outline the type of observations to be included in the study obvious difficulties arose. Personality is difficult to define even in older children. Generally it is defined in terms of the predominant characteristics the individual displays. Thus one child is called egocentric, another introverted, and so on. Such a characterization of personality generally does not include an evaluation of the patterns of personality. Often the predominant characteristic used to describe a personality is one which either causes inconvenience to others or disturbances of the individual's emotional balance. It is therefore obviously much more difficult to describe the personality of the newborn infant than the older child, because his social reactions are not as yet fixed. For this reason definite items were arbitrarily chosen for the characterization of the infant's personality.

As the experimenters were unable to spend much time in the nursery, the nurses were asked to make a number of observations.

Nurses often classify infants as "good" or "bad." When asked to list the qualities of a good or a bad baby, however, they usually give generalities such as, "He is just mean," or, "She is such a sweet little thing." The nurse was therefore asked to check on a printed form a list of specific items at specific times. These items included such terms as "quiet," "crying," "wet," "dry," "irritable," and so on. The nurses usually attended and observed the infants in the nursery at approximately 7:00 a.m., their reactions to bathing and dressing between 7:00–10:00 a.m., and their reactions at the ten o'clock feeding.

One hundred sixty nine infants were observed, and a total of 1037 observations were made, the number of observations per infant ranging from one to nineteen. An observation included a record of several activities, such as "quiet" or "crying," condition at feeding time, reactions during bathing and dressing, and "wet" or "dry." If any one or all of these items were checked on a given day, a single observation was recorded. Very few infants were observed on the first day and most of them left the hospital on the tenth day. Thus a complete set of observations for the average infant included in most instances only nine consecutive days. Thirteen of the 169 subjects were observed for ten days or more, while thirteen were observed only once. More than 100 of the subjects had five or more consecutive observations.

TABLE 28

Observed behavior of infants during bathing and dressing

AGE	QUIET	CRYING	IRRITABLE
days			
2	45	46	3
3	53	46	3
4	48	51	8
5	42	56	11
6	52	42	2
7	42	54	7
8	37	44	4
9	41	37	9
10	36	44	4
Above 10	58	27	11
Ages 1–7	240	241	27
Ages 7 and older	214	206	35
Total observations..	454	447	62

When nurses were questioned concerning the behavior of infants during bathing and dressing, they differed greatly in their opinions. Some said that all babies cried during the bathing period, whereas others maintained that infants in general were quiet and "enjoyed bathing." Table 28 presents the results of the observations during bathing and dressing. There were 454 instances during which infants were quiet during bathing and dressing, and 447 of crying. This difference does not appear to be significant. When the observations were separated into two age groups, it was found that in the first six-day period, 240 were quiet and 241 cried. Of the infants older than six days 214 were quiet and 206 cried. These data indicate that an infant selected at random is just as likely to be quiet as he is to cry during the process of bathing and dressing. There seemed to be no change with age during the ten-day period when the group as a whole was considered. Similar observations at feeding time are summarized in table 29.

TABLE 29

Observed behavior of infants before and during feeding

AGE	QUIET AT FEEDING TIME	CRYING AT FEEDING TIME	ITTITABLE AT FEEDING TIME	FEEDING SPONTANEOUS	FEEDING URGED
days					
2	26	23	4	16	21
3	26	22	9	13	22
4	31	28	4	23	16
5	29	28	5	26	17
6	25	24	6	19	16
7	22	33	1	19	12
8	21	25	2	22	9
9	19	25	2	26	5
10	22	22	4	38	6
Above 10	54	30	4	30	14
Ages 1–7	137	125	28	97	92
Ages 7 and older	138	135	13	135	46
Total...........	275	260	41	232	138

Table 29 shows that a slightly larger number of infants were quiet at feeding time than crying, 275 and 260 respectively. Of the infants under seven days old 137 were quiet and 125 crying at feeding time. Of those seven days or older the corresponding figures were 138 and 135. These differences do not appear to be significant.

These findings contradict the common belief that infants generally show their discomfort just before feeding time by crying. Even the nurses who were in charge of these infants expressed the opinion, before the observations were tabulated, that most infants show their hunger by crying. In some cases it was observed that the infant did not cry when feeding was delayed five or ten minutes. No attempt was made to delay the feeding period, but in a few cases when feeding was inordinately delayed a good deal of crying and irritability were observed.

TABLE 30

*Number and per cent of infants quiet, wet, dry and crying, according to the observations of graduate nurses**

AGE	QUIET		CRYING		TOTAL	DRY		WET		TOTAL
	Number	Per cent	Number	Per cent		Number	Per cent	Number	Per cent	
days										
1	1	50	1	50	2	3	43	4	57	7
2	29	60	19	40	48	44	48	47	52	91
3	27	63	16	37	43	39	41	57	59	96
4	26	65	14	35	40	37	37	63	63	100
5	21	51	20	49	41	30	31	67	69	97
6	20	53	18	47	38	25	26	73	74	98
7	23	56	18	44	41	23	25	70	75	93
8	23	61	15	39	38	16	20	65	80	81
9	25	64	14	36	39	18	23	62	77	80
10	29	67	14	33	43	15	19	63	81	78
Above 10	38	76	12	24	50	15	18	67	82	82
Total....	262	62	161	38	423	265	29	638	71	903

* All recordings were used in this table without regard to completeness for any given infant. Some of the records covered one day while others were for the full ten-day period. More of the infants were checked for wetness or dryness, as the totals show, than were observed for crying or quiet.

Twenty-eight infants under seven days of age were found to be irritable at feeding time, whereas only thirteen infants older than six days were found to be irritable at this time. Apparently the establishment of the feeding time (and habit) in older infants makes for decreased irritability.

It is striking that the number of infants requiring urging at feeding was much greater among the younger infants, and that the number feeding spontaneously increased with age. No doubt this was partly due to the inadequacy of the sucking reflex in the young infants. It is well known that the newborn infant frequently has to be taught to take the breast. Often the nurse moves the infant's chin up and down, attempting to initiate the act of sucking. It is thus not unusual to find that spontaneous feeding increases with age.

The number of infants quiet or crying when observed while in their cribs is recorded in table 30. Sixty-two per cent were quiet and 38 per cent were crying when observed.

It is probable that during the first five days there are difficulties of adjustment to food which may cause a temporary increase in the per cent of infants crying. From the fifth day on the per cent crying steadily decreased and the per cent quiet increased. By the tenth day 67 per cent were quiet, and above ten days 76 per cent were quiet.

The curves in figure 18 show that quiescence and wetness increased together. Therefore, crying and dryness must decrease together. These results do not mean that quiet babies are wet, and crying babies dry. They do show, however, that many quiet babies are wet, since quiescence and wetness were at every age found in more than fifty per cent. Wetness increased rather regularly up to the eighth day, when eighty per cent were observed to be wet. Approximately four-fifths of the infants past the eighth day were wet when observed.

Mothers and nurses may believe that infants are usually wet when observed at random, but the results show that at least one in five will be dry at any given time during the first day of life. With advance in age, however, the per cent of dryness decreases. Wetness is probably associated with the intake of liquids; thus it increases until the eighty per cent level has been reached.

The relationship of wetness and dryness to crying and quiescence can be seen in table 31. The results show that 67 per cent of those infants who were quiet were also wet, and 33 per cent were dry. Eighty per cent of those who were crying were wet and 20 per cent dry. These figures show that there is a direct relation between crying and wetness even though the majority of the quiet group were wet. The evidence does not make it possible to determine whether an infant cries because it is wet or wets because it cries. Experience with older children, however, leads one to suspect that the major portion of the excessive wetness among the crying group is due to the crying. Wetness may cause some newborn babies to cry but it seems likely that the crying causes more of them to wet.

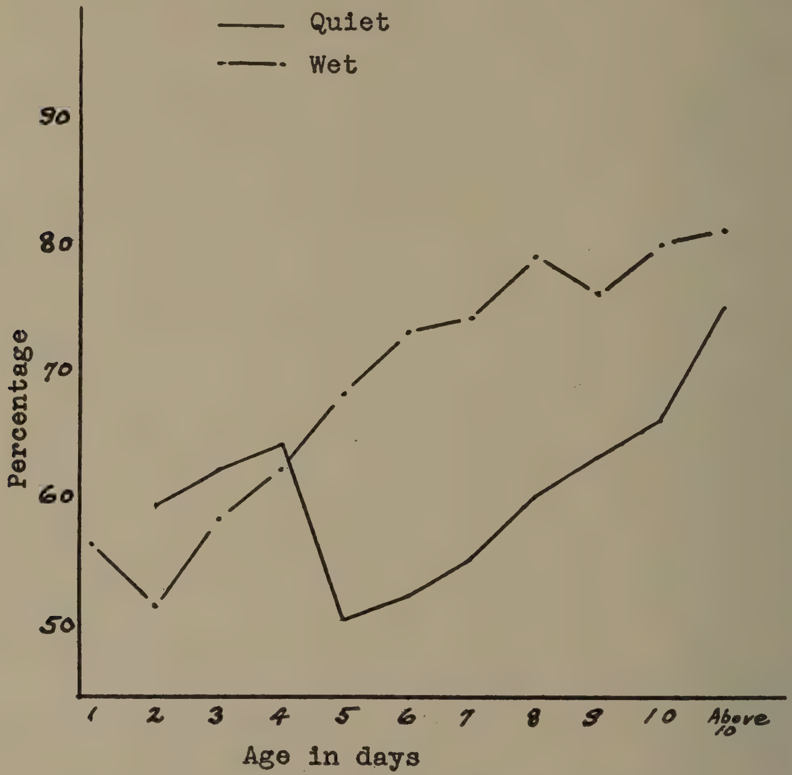

Fig. 18. Distribution of Quiet and Wet According to Age

Considering the group of 357 subjects as a whole, 44 per cent were quiet and wet, 21 per cent were quiet and dry, 28 per cent were crying and wet and 7 per cent were crying and dry. Fully one-third more were quiet and wet than were crying and wet, while three times as many were quiet and dry as were crying and dry. Nearly one-half of the group were quiet but wet. The most common condition of an infant is, therefore, quiet but wet.

It is known that girls exceed boys in some phases of physiological development even at birth. Studies of ossification have shown that females exceed males in their development at every age from birth to maturity. It is possible, then, that differences may exist in their behavior at birth. Table 32 presents comparative data for males and females with reference to crying, quiescence, wetness and dryness. Records used in compiling table 32 were only of infants who had been observed five or more consecutive days. These data show that 44 per cent of the girls were crying and 56 per cent were quiet whereas 29 per cent of the boys were crying and 71 per cent were quiet. Approximately one-third more of the girls than of the boys were crying. The percentages of wetness and dryness were 77 and 23 for girls and

TABLE 31

The relation of wetness and dryness to quiescence and crying

AGE	QUIET		CRYING		TOTAL
	Number wet	Number dry	Number wet	Number dry	
days					
2	14	11	12	3	40
3	10	17	10	4	41
4	15	7	8	2	32
5	15	2	9	4	30
6	11	7	9	6	33
7	15	8	13	0	36
8	19	6	11	0	36
9	19	4	10	3	36
10	17	5	11	1	34
Above 10	22	10	6	1	39
Total	157	77	99	24	357
Per cent	44	21	28	7	100
Per cent of those quiet	67	33			
Per cent of those crying			80	20	

72 and 28 for boys. Since a larger percentage of girls were crying and since crying was related to wetness, it was expected that more of the girls would be wet. Wetness or dryness is not the major factor in this comparison.

Inconstant responses from day to day seem to be rather typical of newborn infants. Shirley (35) states that no infant represents a definite type of personality, but that major characteristics of personality are observed in early infancy. Our findings do not corroborate such an inference. It is possible, however, or even probable, that after the ten-day period definite characteristics of personality manifest themselves. This does not mean that a given child does not show constant and definite personality manifestations even during the first ten days of life. Indeed, previous observations by the authors, and observations during the present study tend to show that some children manifest rather constant characteristics of personality early in life. Nevertheless, when a statistical evaluation is made of a large number of observations it is impossible to observe a constancy of personality pattern in most infants as measured by overt reactions defined in this study.

TABLE 32

*The relation of the sex of the infant to crying, quiet, wet and dry**

	GIRLS		BOYS		TOTAL	
	Number	Per cent	Number	Per cent	Number	Per cent
Crying	60	44	54	29	114	35
Quiet	75	56	130	71	205	65
Wet	352	77	269	72	621	74
Dry	107	23	106	28	213	26

* Records of infants who had been observed on five or more consecutive days.

The inconstancy of the reactions of just-born infants was also observed in their responses to test situations. When repeated tests were made on given infants it was found that these responses varied as widely from day to day as the variation between any two infants. It is probable that the environment is not sufficiently complex and differentiated during the first ten days of life to cause personality differentiation except in a small percentage of cases. Later, with environmental conditioning, distinct differentiation occurs, and personality fixation appears.

RESPONSIVENESS AS A BEHAVIOR PATTERN

As previously mentioned, the nurses who took care of the infants generally classified them as either "good" or "bad" depending upon their irritability and frequency of crying. An attempt was made to obtain such a classification of every infant examined. As a result, sixty-one infants were classified as "good" babies. This classification was not accepted unless there was a uniformity of opinion among the nurses who observed the infants. The responses of these sixty-one infants were tabulated separately and compared with the responses of the entire group.

TABLE 33

Size of pupils of two groups of infants

SIZE OF PUPIL	AWAKE		ASLEEP	
	"Good" infants	Entire group	"Good" infants	Entire group
	per cent	*per cent*	*per cent*	*per cent*
Small	42.8	19.6	40.0	44.4
Moderately small	28.6	10.7	20.0	18.5
Moderate	14.3	14.3	40.0	18.5
Large	14.3	28.6	0.0	7.5

Table 33 presents the data for pupillary size of the "good" infants and the entire group. It is seen that when the infants were awake 42.8 per cent of the "good" infants had small pupils compared with 19.6 per cent of the entire group. Twenty-eight and six-tenths per cent of the "good" infants had a moderately small pupil, whereas only 10.7 per cent of the entire group had moderately small pupils. The percentage of moderate size pupils was the same in both groups and the percentage of large pupils was smaller for "good" infants than the entire group. Of the group examined when asleep, the per cent of small pupils was practically the same in the "good" infants as in the entire group. Thus in general the "good" babies when awake tended to have smaller pupils than the group as a whole.

It was previously seen that small pupils are characteristic of sleeping infants. It may be that the size of the pupil is related to the alertness of the infant, which perhaps accounts for the decrease in size with sleep. "Good" babies, even though awake, resemble in many ways the average sleeping infant, especially in so far as alertness is concerned, and this may explain the difference in the size of their pupils from that of the average infant. When eye movements were examined, it was found that the per cent of incoördination of both eyes of the "good" babies was 6.0 per cent, compared with 8.8 per cent for the entire group. This difference is not significant, as the probable error of the difference was 2.6.

TABLE 34

Mean age for minimum stimulus necessary for good pupillary reflex

	RIGHT EYE			LEFT EYE		
	Stimulus					
	3 c.p.	6 c.p.	12 c.p.	3 c.p.	6 c.p.	12 c.p.
"Good" babies	161*	149	121	170	125	118
Entire group	134	133	81	136	116	83

* Mean age in hours.

TABLE 35

Response of pupils of two groups of infants to light

	3 C.P.		6 C.P.		12 C.P.	
	None	Good	None	Good	None	Good
"Good" babies	135*	181	117	141		119
Entire group	97	135	78	118	56	115

* Mean age in hours.

Table 34 shows the minimum stimulus which produced a good pupillary response, according to age. It is seen that the age of the "good" babies for each of the three intensities of stimulation was higher than for the entire group. In other words, the mean age of the "good" babies was greater than that of the general group, before they gave a good response to the same stimulus. For the right eye, the mean age was 161 hours for 3 c.p., 149 hours for 6 c.p., and 121 hours for 12 c.p., compared with 134, 133, and 81 hours for the entire group. A similar relationship is seen in the responses of the left eye.

When the responses of the pupils were classified into *none* and *good* (table 35), "good" babies were, in all instances but one, older than the average of the entire group before they gave a good response. Thus, for 3 c.p., the "good" babies gave a good response at the mean age of 181 hours, compared with 135 hours for the entire group; for 6 c.p., 141 hours, compared with 118 hours, and for 12 c.p., 119 hours, compared with 115 hours. Furthermore, the pupils of the "good" babies gave no response to light stimuli at a later age than did the pupils of infants in the group as a whole.

TABLE 36

Per cent of defense movements in response to pressure stimulus

	"GOOD" BABIES	ENTIRE GROUP
Right hand	19.8	18.1
Left hand	21.2	21.3
Both hands	3.4	5.2

TABLE 37

Minimum pain stimulus (needle) for a response

	FACE			LEG		
	Stimulus					
	1	1½	2	1	1½	2
"Good" babies	140*	121	143	150	125	155
Entire group	116	98	88	114	101	89

* Mean age in hours.

The defense movements of the "good" babies were also compared with the defense movements of the entire group. Table 36 presents the comparative data. No significant differences were found.

Table 37 presents the data for the minimum pain stimulus necessary for a reaction. It is seen that the mean age of the "good" babies was higher for each of the three intensities of stimulation. Thus, for the stimulation of the face, the mean age to stimulus intensity 1 was 140 hours, to 1½, 121 hours, and to 2, 143 hours, compared with the mean ages of the entire group, namely, 116, 98, and 88. A similar relationship was found in the responses to stimulation of the leg. The responses of the two groups of infants to pain stimuli corresponded to the relative responses of the pupils.

When the strength of grasp was analyzed, it was found that the average strength of grasp of both the right and left hand of the "good" babies was greater than the averages for the entire group. Because of the difficulty of interpreting the grasp reflex in so far as strength is concerned, no attempt is made to account for this difference. It is probable, however, that the difference between the two groups was not statistically significant. For the "good" babies the average strength of the right hand was 1882 grams, compared with 1762 for the entire group, and the average strength of the left hand was 1802 grams compared with 1766 grams.

In summary, the pupils of "good" infants when awake tend to be smaller than those of infants in general, when awake. A small pupil is characteristic of the sleeping infant. Further evidence that the good infant resembles the sleeping infant in lack of responsiveness to stimulation is the fact that he is older than the average infant before his pupillary responses and responses to pain stimuli are equally adequate. Apparently the difference is one of sensitivity rather than motor inadequacy, for "good" infants made coördinated movements of the eyes and defense movements of the arms and hands equally as well as the average.

CHAPTER IX

SUMMARY

1. Quantitatively calibrated stimuli are easily applied to newborn infants, and the responses can therefore also be quantitatively measured and treated statistically.

2. The pupillary reflex increases in adequacy with age. For any given age the adequacy of the reflex is greater the greater the intensity of the stimulus. For any given stimulus intensity, the adequacy of the reflex increases with an increase in age. Coördination of eye movements is the rule in newborn infants. The per cent of incoördination decreases, however, with an increase in age. Fixation of one eyeball and "pursuit" movements of the other eyeball are frequently seen in infants up to ten days of age.

3. Reactivity to a pain stimulus increases with an increase in the age of the infant. For a given intensity of a minimum pain stimulus the number of responses increases with age; for a given age the number of responses increases with an increase in the intensity of the stimulus. The cephalic end of the infant is more responsive to a given pain stimulus than the caudal. The typical reaction to a pain stimulus (needle) applied to the face is a crossed-flexion response of the arm; the opposite arm and hand are brought up to the point stimulated.

4. Defense movements of the arms and hands increase in adequacy, with some irregularities, with an increase in age. The accuracy of the defense reactions also increases with age; thus, those infants who grasped or pushed the instrument from the face were over fifty hours of age. A variety of associated movements occur in response to a pressure stimulus applied to the face, such as arching of the back, attempts to turn the head and kicking.

5. A high correlation exists between the number of leg movements and the number of arm movements. The correlation between the number of defense movements of the arms and the

number of leg movements is somewhat lower, but is also significant. The number of significant leg movements increases with age to 200 hours and then decreases. The strength of the leg movements also increases until the age of 200 hours and then decreases.

6. The average strength of the grasp reflex of the right hand was 1732 grams and of the left 1765 grams. Ten and one-tenth per cent of the infants lifted themselves with the grasp of the right hand, and 10.2 per cent with the left hand. The results of the tests on seventeen infants older than seventeen days showed that the grasp reflex begins to wane at about the eighth week. The strength of the grasp reflex was greater when an infant cried and decreased when an infant was asleep.

7. Ankle clonus was found in over fifty per cent of the cases examined; the Rossolimo sign was found in 72.5 per cent of the cases examined. The frequency of the Babinski reflex is determined by the methods of examination, by the condition of the infants and by the criteria employed. The frequent associated movements are probably defense responses.

8. Behavior patterns of infants are inconstant. Regarding specific behavior items, an infant is as likely to cry as to be quiet, and as likely to be wet as dry when examined at any given time. With age the frequency of quiet and of wetness increase. The infants who were classified as "good" babies by the nurses were less responsive to a number of the stimulating conditions than the entire group.

9. Sensori-motor and defensive responses of newborn infants are probably dependent upon sub-cortical processes. These responses change in type as cortical dominance develops.

CHAPTER X

Theoretical Considerations

In evaluating the findings of this study many problems presented themselves regarding the relative influence of subcortical and cortical dominance as they affect various developmental processes. This study is preliminary to a more comprehensive investigation which will include observations of older infants. The implications of this study in regard to the development of the learning process as related to the problem of cortical dominance will be studied further. The data thus far obtained are naturally not conclusive, partly because of the age limitations of the infants and partly because certain problems which presented themselves could not be investigated at the time this study was under way. The following theoretical considerations are therefore presented in part to illustrate the investigative possibilities of studies of this nature and to propose given theoretical implications to which this study seems to point. These theoretical considerations are based in part upon the interpretation of the findings of this study and in part upon what is known of previous investigations of animals and of infants.

Sufficient evidence has been presented in the literature to show that the newborn infant is not a totally helpless individual. The findings of various experimenters have shown that the newborn infant is equipped with a fairly large repertoire of reactions. These reactions are relatively simple and, as many psychologists have stated, they are often overlooked because the newborn lives in a highly protective and elemental environment. Parental protection, which in a rough way increases with ascent in the phylogenetic scale, shows itself in its most highly evolved form in man. It is but logical to expect, therefore, that the newborn infant requires only the simplest overt skeletal activity in order to maintain itself during the early stages of life.

The responses of the newborn infant on close scrutiny are not as chaotic and undifferentiated as some observers have reported. As we have seen, the newborn infant is equipped with a large number of reflex and defensive responses. These responses can not be seen upon casual observation. The ability of the newborn infant for adaptive activity therefore can not be estimated by observing him in the usual protective nursery environment where all his needs are taken care of. Bühler states, for example, that the behavior of the newborn infant can be judged only by observing him without artificial stimulation. This might be the proper procedure were it not for the fact that the majority, if not all, infants live in a highly protective environment. Irwin states that he has not observed specific defense reactions in newborn infants, although he has found many other adjustive responses. A similar lack of adjustmental reactivity would be observed both in animals and mature human subjects if conditions were made so simple that potential adjustmental responses were not necessary. Potential abilities must be experimentally elicited by specific stimulation.

The original reflex and defense reactions observed in the just-born infant develop in adequacy with increase in age. Thus we have found in this study, for example, that the adequacy of the pupillary reflex and the reaction to a pain stimulus increases with age. As a corollary of these observations, the reactivity of an infant, whether reflexive or defensive, is greater the more intense the stimulus. The data on pupillary responses showed, for example, that the mean age for a good response to a 3 candle power stimulus was 134.2 hours, to a 6 candle power stimulus, 121.1 hours, and to 12 candle power, 110.5. Similarly, differences in the extent of reactivity of the pupils were observed in response to a given stimulus at different ages. To a 3 candle power stimulus, for example, the mean age of the infants who did not react was 97.6 hours, the age when a fair response was obtained was 111.7 hours, and the age when a good response was obtained was 134.2 hours. The respective ages for these types of responses, when a 6 candle power stimulus was used, were 78.9, 95.3, and 121.1. Thus it is seen that the adequacy of the pupillary response not only increases with age but that the age for a response also decreases with an increase in the intensity of the stimulating condition.

Similarly, the mean age of infants responding to a pain stimulus decreased with an increase in the intensity of the stimulus. This was observed both when the stimulus was applied to the face and to the leg.

It is difficult to interpret the development of the reflex and sensori-motor responses. Do they increase in adequacy in the same way that other adjustmental reactions thus increase? Or is the increase in adequacy related to the development of the conduction possibilities of the nervous system? On the basis of the evidence presented by Feldman, Langworthy, and others, it may be assumed that the nervous system involved in such reactions is capable at birth of transmitting and conducting the impulses. The increase in reactivity is therefore not due entirely to an increase in the organic potentialities of the conduction pathways. It must then be assumed that a functional integration of the pathways involved in these simple reflexive and sensori-motor reactions gradually takes place. As we shall show later, the more complex responses which are integrated and controlled by cortical processes also increase in adequacy, and change qualitatively in nature as a result not only of an organic integration but also of a functional coördination of the nervous pathways involved.

In Chapter IV mention was made of the work of Irwin. He maintains that the characteristic activity of the newborn infant may be described as mass activity made up of uncoördinated, irregular, undefined muscular responses. The coördinated adjustmental reactions supposedly develop out of this mass activity. In part this means that the newborn infant is unable to react with precision to ordinary stimulating conditions. The large number of observations of this experimental study, and the evidence of other studies show, however, that the theory of mass activity, in so far as it is related to the adjustmental possibilities of newborn infants, must be radically modified. Although the newborn infant does preponderantly make uncoördinated movements, these movements are not "mass" activities but are reactions which the infant can not integrate in response to stimuli. In spite of the large number of undirected movements, the infant does make many directed movements in response to stimuli of an optimal sort.

That newborn infants make undirected movements is not surprising. Similar undirected movements are made by older infants and children in their attempts to adjust for the first time to a new situation. Thus observations have shown that a child learning to write at first makes many undirected and diffuse movements. The stimulating conditions which are directed toward a writing reponse are followed by a diffusion and perhaps a disorganization of nervous impulses, resulting in a diffusion of muscular responses. There are, however, significant differences between the diffusion of responses of newborn infants and those of children when they attempt to learn a complex process. As we shall see later, the diffusion responses of children are relatively rapidly replaced by directed and voluntary activities. The first responses of newborn infants differ in many respects from the activities in a learning process of children.

Many experimenters in the field of infant development believe that the newborn infant can be regarded as a "sub-cortical animal" whose activities have their centers in the phylogenetically and ontogenetically oldest parts of the brain. They point to the frequency of pathological reflexes, the inadequacy of the reactions and the relatively meager repertoire of responses of the infant as evidence for this belief.

The evidence from this experimental study as well as previously published reports of the authors indicates that the belief that a newborn infant is sub-cortically dominated is valid. Mention has already been made of the increase in adequacy of reflexes with age. In addition, the character of the reflexes of infants shows that cortical function has not been fully assumed in the newborn infant as an integrative process. Thus the positive Babinski is found in newborn infants as well as a surprisingly large number of instances of ankle clonus and the Rossolimo sign. The existence of given crossed reflexes also is evidence of predominant sub-cortical activity. In this study the crossed reflex was found to be the most typical response to a pain stimulus applied to the face. The anatomical location of the pathways involved in the crossed reflex response to a pain stimulus is evidence of the dominance of subcortical centers.

The presence and character of the grasp reflex in the newborn infant perhaps offer some evidence of the change of nervous system dominance with advance in age. The data presented showed that the right hand does not dominate in terms of strength. Indeed, it was found that the left hand is on the average slightly stronger. The majority of older children are predominantly right-handed in all activities related or unrelated to the grasp reflex. With advance in age there is apparently, therefore, a shift in the central nervous system function.

Incidentally, it was observed that the newborn infant tends to be somewhat "left-sided" in other respects. For example, there was a somewhat more adequate reflex pupillary response of the left eye than the right, in that a good response of the right pupil on the average appeared somewhat later than the left. While these differences are only slight in some instances, they were consistent and therefore probably of some significance. The average per cent of defense movements of the left hand in response to pressure on the chin also exceeded the right. This difference was particularly striking in those infants who made excessive kicking movements in response to the pressure stimulus. This type of remote reaction, lacking the specifically defensive character of arm movements made in response to the same stimulus is probably to be regarded as of "lower" order. If so, the difference in the adjustmental reactivity of the two hands in this instance offers further evidence that the more primitive the reactions of the infant, the more "left-sided" they tend to be. The strength of leg movements in response to the pressure stimulus was in most instances stronger on the left than the right. On the whole, these observations show that a newborn infant is not dominated in his responses by the usual asymmetrical cortical function manifested in mature individuals.

Even the defense movements of the newborn infant may be considered more dependent upon sub-cortical control than upon the cortical control evident in the reactions of older children which are similar in nature to the defenses of the newborn. As we have seen previously, these defenses are different in type from many of the adjustmental responses of older children. They are direct, highly coördinated reflex reactions, functionally designed to remove a noxious stimulus. Despite the existence of many undirected activities throughout which the coördinations are interspersed, the defense reactions are apparently not acquired entirely by the trial and error method which is characteristic of many of the responses of older children. The reactions of older children which are acquired by the trial and error method exist alongside of reflex activities, although some of the original reflexes are replaced. This is not contradictory to the evidence that adjustmental responses of even the most elemental type develop in adequacy with age, for it has already been shown that sub-cortically dominated reactions may increase in adequacy without assuming that cortical processes take a predominant part in their manifestations. It is also possible, though perhaps not entirely probable, that most of the muscular responses of the newborn infant to a noxious stimulus would take the form of coördinated defenses were it not that a great deal of diffusion takes place in response to most stimuli. An example of this diffusion which interferes with adjustmental reactions is seen in the response to a strong pressure stimulus on the chin. When the pressure stimulus is above 1,000 grams, a very frequent response of the newborn infant is an arching of the back such that he supports himself upon his heels and head. The arms are likely to be held rigidly in a flexed position, but at times are waved about, seemingly without definite direction. Again, when a strong pain stimulus is applied, diffusion takes place to a much greater extent than when a less intense stimulus is applied.

The number of undifferentiated movements is greater not only when the stimulus is intense but also when it is suddenly applied, which perhaps has the same significance as an intense stimulation. That there is little relation between the number of undifferentiated movements and the coördinated defenses of the arms and hands, is shown by analysis of the reactions to a pressure stimulus on the chin. The coefficient of correlation between the number of movements and the per cent of defenses of the right arm and hand was 0.08, for the left hand, 0.11, and between total movements and per cent of coördinations, 0.07. It is extremely difficult to gauge the optimum stimulus and it is possible that the pressure employed caused a diffusion of muscular responses. Even ordinary external stimulation naturally arising under normal nursery conditions may result in a diffusion of impulses giving rise to what appears to be generalized activity. When an infant is brought into a bright light, for example, the lids close quickly, and the infant often becomes restless. When the temperature of the room is below 74° the infant may appear irritable and restless. It is therefore not unreasonable to assume from these incidental observations that a number of noxious stimuli of accidental origin may be present, causing undifferentiated activities, stimuli which are neither qualitatively nor quantitatively observed by experimenters.

In contradistinction to the type of defense reaction seen in the newborn infant, the defense coördinations and other adjustmental responses of older children appear to be of a different order. In the coördinations of older children, learning of the ordinary sensori-motor type takes place by process of trial and error of varying degrees of extensity. Some of these learning processes are temporally brief, whereas others are lengthy. In these learning processes gradual control is attained, whereas the responses of the newborn infant which appear to be controlled are immediate and are apparently perfected, in so far as adequacy is concerned, as soon as they appear.

In the process of mental and chronological growth, a sequence takes place in the development of sensori-motor and other activities. This sequence is accompanied, if not determined, by a gradual assumption of cortical dominance. This assumption of dominance by the cortex is not the result entirely of structural growth. We know, for example, that practically no new cells develop in the cortex following birth. There are, however, some other forms of structural development and structural integration, such as myelinization of various centers. Cortical integration and the assumption of dominance are, however, in a large part, functional as well as organic processes. We have seen, for example, that the infant shows many abnormal reflexes which are the result of the lack of complete function of the pyramidal tracts. Yet the nervous system, including the pyramidal tracts, is sufficiently developed anatomically at birth to allow the transmission of impulses. This Feldman has shown and Langworthy quotes much evidence for the structural integrity of the nervous system of the newborn infant. He concludes from his studies of the behavior patterns and myelinization of the nervous system in the human fetus and infant that by the time of birth the development of myelin is such that all the activities can be mediated by neural pathways which have acquired their myelin sheaths. The disappearance of the pathological reflexes and the appearance of normal responses must therefore be considered due to a functional integration of the pyramidal tracts. The explanation must further involve a description of cortical integration.

If functional integration is a necessary prerequisite to the assumption of normal responses mediated by the pyramidal tracts, it is also safe to assume that other cortical functions are influenced by similar integrations. It is known from the work of Flechsig and others, for example, that some anatomical development takes place following birth. Nevertheless, many functions are not assumed when the cortex matures anatomically. Concomitant with the anatomical maturation of whatever sort takes place, integration begins and develops in a more and more complex manner manifesting itself in complex responses which might have been possible at an earlier age if dependent purely on a gross structural basis.

According to Lashley (21), there is a functional organization of the cortex independent of structural development. The plasticity of the nervous system and the complexity of its interacting mechanisms do not cease with the completion of gross development. Others have also called attention to the functional organization of the cortex independent of gross structural development. From the histological standpoint, for example, there is little evidence of a gross structural difference between the brains of retarded and normal children.

In the case of organic dementia, such as that due to senile changes, the structural disturbance is usually so diffuse and often quantitatively extensive that a disturbance of cortical function might be expected. Furthermore, it is well known that cortical integration is likely to be disturbed when the interdependent relationships of the functional and structural systems are unbalanced.

The development of cortical function is a gradual integrative process, probably beginning early in the fetal stage and gaining momentum as structural integration increases. As functional cortical integration becomes more and more complete, mental processes of a higher order are made possible. At first cortical integration (anatomical and functional) allows for the establishment of the normal reflexes. Cortical control of the original subcortically dominated reflexes allows for a variety of combinations resulting in adjustmental responses which may still be of the reflex type but are now sufficiently variable to adjust the individual to a more complex stimulus-response relationship. The cortex now assumes the function of inhibitory and regulatory control, as Herrick (17) and others have shown. Following the establishment of a variety of intricate responses which are still of the sensori-motor order but which are cortically dominated and different in appearance from the original sensori-motor responses which were subcortically dominated, a series of motor phenomena are established characterized principally as delayed responses. When these activities are firmly established, and only then, abstract and symbolic mental processes appear. There is, or course, a good deal of overlapping in the development of individual children, and the stages of growth are not clearly defined.

The progress from sub-cortical to cortical dominance is seen in the normal process of the mental growth of every child. As we have seen, a sequence takes place in the development of even the simplest sensori-motor activities. The sensori-motor reactions of the newborn infant which are essentially of the immediate defense type, the function of which is very similar to, if not exactly the same as the defense reflexes of lower animals, finally are replaced by more complex sensori-motor activities. In some respects, for example, the crossed reflex response of the hands of a newborn infant to a pain stimulus is not unlike, in terms of accuracy, the scratch reflex of the pithed frog as it removes the noxious stimulus of acid placed on its skin.

As the infant matures, other types of sensori-motor responses gradually develop, widening the scope of adjustment and therefore increasing intellectual ability. Some of the first coördinations which seem to be of the voluntary and therefore of the cortically dominated type can still be classed in the same functional group as the early sensori-motor reactions. The attempts of the infant to hold up the head, later to right itself quickly when in an awkward position, and still later to sit up, are activities which have replaced, but are not much more advanced than some of the original defense and righting activities, examples of which are seen in the responses to stimuli of pain and pressure. The grasp reflex of the newborn infant is probably in some respects a righting reflex, the function of which is later replaced by other forms of righting activities. That the original righting reflexes are almost entirely sub-cortical, is further shown by the results of experimental work on monkeys and by observations of the behavior of human subjects with cortical lesions. Experimental lesions of given parts of the cortex of the monkey produce forced grasping. In man forced involuntary grasping is also produced by given pathological conditions of the cortex. These involuntary grasp movements are genetically probably of the same origin as the grasp reflex of the newborn infant.

Bucy (6) states that pre-motor area 6 is primarily concerned with the integration of complex movements, and that it exerts an inhibitory influence over the subcortical areas concerned primarily with the postural and righting reflexes. These original righting and defense reactions must necessarily disappear as integral functions with the assumption of cortical dominance, since the other types of sensori-motor responses which gradually replace them would be impossible because of mutual interference.

With the perfection of the second and higher type of sensori-motor activity, the child is now ready to begin its mental functions on the higher or symbolic plane. In this third process we see the development of conceptual and abstract mental activity.

The development of speech as a symbolic process may in part be considered as a complex associative process developing subsequent to a given level of sensori-motor response. This does not mean that the various phases of growth are sharply delimited. On the contrary a good deal of overlapping is observed in the growth process, but each phase facilitates the subsequent development of another phase. The adjustment of the newborn infant by means of sensori-motor responses can not go on indefinitely. The sensori-motor development is not only a factor in the growth of intelligence but is also that growth in its early manifestations. Many sensori-motor responses become coördinated and integrated quite early and thus are not capable of further development. A new method of utilizing these reactions through the combination of muscular movements then develops. Muscular responses, however, can not continue to increase in complexity indefinitely because of many limitations. In time the sensori-motor responses and their combinations are not sufficient to adjust the infant, and symbolic speech makes possible complex adjustments which the child would otherwise be unable to make. By means of language, highly complex forms of behavior are possible with much less effort and less time than by means of sensori-motor activities. Language provides a much finer means of adjustment than the slower and more cumbersome activities which were effective for adjustment in the early stages.

Intricate interrelationships no doubt exist between the development of speech as a symbolic process and the growth and modifications of sensori-motor activities. It is our plan to continue our investigations in the attempt to discover some of the factors involved in this relationship.

As already intimated, symbolic functions are closely related to the second type of sensori-motor adjustment to which reference was previously made. Thus, when the child is retarded in developing the higher combinations of sensori-motor reactions, his mental growth in the conceptual and abstract realms is also retarded. The retardation appears to be proportional, but it is not known exactly what the proportion is. The child who walks at eighteen months develops an intelligence greater than the child who first learns to walk at two years, and still greater than the child who walks at three years. The only exception to this gradual and orderly sequence of development is seen in the gifted child in whom Terman (36) has shown that talking precedes walking by a few weeks. Taking this exception into account it is nevertheless seen that within a given process a certain degree of sensori-motor development precedes the manifestation of symbolic mental processes. As Gesell has shown, a definite sensori-motor pattern is seen in the normally growing child. If this pattern lags, the later growth of the child is impaired. It is not too far afield to state that the retardation of the basic sensori-motor responses indicates a lack in the degree of cortical dominance without which conceptual and mental life is impaired.

Workers in child development have noticed a relation between some forms of sensori-motor disturbance and retardation of intelligence. In most of these cases the intellectual defect is not great and is at times accompanied by speech disturbances. These sensori-motor inadequacies show themselves especially in defects in complex manipulatory skills. In a large number of these cases the neurological diagnosis is some form of brain injury which affects cortical activity.

This mechanism is illustrated in children who appear to be normal during the first two or three years of life, but who are found to be retarded when put to mental tasks such as those required in school activities. The following two cases are presented as suggestive of the mechanism under discussion. In the case of one boy of six, the diagnosis was an arrested hydrocephalus. The parents, who were intelligent, had observed him carefully from birth. They stated that he developed normally, that he walked and talked at the usual time, but that his speech became somewhat garbled and unintelligible when he was about three years of age, when he first began to use language of a comprehensive type. Neurological examination showed no defects.

The sensory processes in so far as they could be mapped accurately in a six-year-old boy, were normal. The strength of the large and small muscles was also normal. His gross sensori-motor responses, that is, his large skeletal movements, were normal. Manipulation was disturbed, however, especially that requiring fine movements. Tests of the usual formboard type showed no retardation when the results were scored in the ordinary manner. He showed great difficulty, however, in manipulating a pencil and in other reactions which required precise manipulatory activities of the fingers. His speech was of the infantile sort but not "baby talk" sometimes found either in defective children or in children who develop given speech habits.

The neurological interpretation of this case was as follows: the hydrocephalus did not progress to a sufficient extent to disturb the cortical condition as it affected the development of the gross sensori-motor activities and the general mental processes. The cortical integration was affected, however, to a sufficient extent to inhibit the proper development of the fine manipulatory processes and concomitantly with this inhibition speech was also disturbed. In consequence the higher mental processes did not develop at the normal rate. The I.Q. of 83 was commensurate with the retardation of the fine sensori-motor reactions and the speech difficulty.

The relationship between sensori-motor abilities and intelligence, as measured in terms of tests and school achievement, was further shown in this boy. By continuous practice in manipulatory activities his reactions became more adequate. At the same time, his speech increased in intelligibility and his school achievement also increased relatively rapidly.

In another case the early history was similar, but the intellectual retardation was greater. Examination of this boy also showed that his finer sensori-motor coördinations were more defective than those of the boy first described, and his language and speech also showed a relatively similar defective development.

When the gross sensori-motor activities of a defective and a normal child are tested, very little difference is found. They are both able to learn simple motor skills equally well except for the difference which one ordinarily finds in perseverance and motivation. When precise manipulatory processes are tested, however, wide differences are found in ability, depending upon the degree of retardation. The difficulty in differentiating children on the basis of complex sensori-motor ability is due in part to the fact that the learning of complex skills involving complex manipulation is determined in part by mental processes of the abstract and conceptual types. The important point is, however, that those abstractions and conceptions which aid the learning of complex manipulatory activities are dependent in part, at least, upon the perfection of the sensori-motor mechanism itself.

It is not implied that complete cortical integration with its regulatory and controlling influences over the sub-cortical areas means that the functions of the sub-cortical areas are always directed. As Herrick has shown, there is a temporal dissociation of cortical from sub-cortical functions through the action of the association tissue which is interpolated between the more primitive cortical projection areas. The complete cortical integration and function thus allows many of the second type of reflex and sensori-motor processes to continue, but never in their dominant or independent manifestations in which they appeared at first. Thus, for example, peripherally initiated impulses are first received and combined in sub-cortical centers. The cortex does not come into play if these lower centers are adequate in determining an appropriate reaction. If the sub-cortical patterns are inadequate, the cortex takes the predominant rôle.[4] In this way functional relationships are possible between the lower sensori-motor processes and the higher symbolic activities. This is further evidence of the various concomitant stages of the growth of adjustmental activities from the primitive reflex reactions to the complex motor, voluntary and symbolic activities, and the gradual assumption of complete cortical integration and dominance.

It is not assumed, however, that cortical function involves only symbolic and conceptual processes since it has been amply shown that motor habits are not possible without fairly complete cortical activity. This Lashley (21) has well shown in his work with rats.

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[4] See C. Judson Herrick, Brains of rats and men, 1930, University of Chicago Press, p. 260.

Lashley (20) and others state that simple habits are acquired by the feebleminded almost as rapidly as by normal children. Although the evidence shows that the rate of learning of complex habits increases with the ascent in the phylogenetic scale, and similarly in the more intelligent children, Lashley questions whether the complexity of a habit is merely a function of the number of single associations required, or whether the influencing factor is a qualitative change or element determining a limit to the learning of complex reactions. Gesell (15) states that the development of prehension habits, such as is illustrated in the prehension of a pellet, takes place not by the coördination of "snatches" of successful acts but by the progressive acquisition of behavior patterns which are the result of developmental increments.

We may therefore assume that cortical function as it unfolds, allows for the assumption, first, of complex muscular combinations, then for the development of substitutive and symbolic behavior as manifested to begin with by the development of words, sentences, and gestures, and then of the more complex mental processes involving concepts and abstractions. The unfolding of these processes may be called learning, since each higher step is dependent upon the completion of the lower. The development of proficiency within each so-called stage probably goes on as a trial and error process not unlike that seen in the learning of some special skill, but each stage is temporally separated from the other, yet interdependent.

The change from sub-cortical to complete cortical dominance is not inferred to be a learning process in itself. It is seen, however, that the process we call learning takes place concomitantly with a shift of dominance. There is probably no real controversy between observers who believe that the development of complex activities of young children takes place through maturation, and those who believe that they are learning processes defined in the traditional manner. Certainly the organic nervous system must function completely, but as cortical function is in process of establishment, including in this function the inhibition of given reactions and the initiation of voluntary activity, the psychological mechanism of learning goes on concomitantly.

Some experimenters maintain that a more direct relationship than has been inferred in this study exists between sensori-motor development and intelligence and learning. Paradines (27) states, for example, that as intelligence increases, the threshold for pain decreases, allowing for a greater adequacy of given types of sensori-motor activities, and therefore allowing for more complex adjustmental reactions. Paradines maintains that this has been found in animal development and also in the early development of infants.

Cortical function and integration is not firmly established even when the first abstract and conceptual mental processes develop. How long functional integration continues is not known, but that it must continue beyond the stage when the child first uses language and concepts cannot be denied. There is probably an interdependent and reversible relationship between the process of cortical integration and the increasing tempo of the learning process, and therefore of intelligence. It is not improbable that the education of a child, even in the most formal aspects, is a means, at least at first, of hastening the integration of cortical processes. The establishment of one order of mental complexity allows the assumption of a higher order. Sufficient evidence has been presented in many studies to show that children living in an environment offering meager educational opportunities (formal and informal) show relatively poor intelligence test performance. Thus, in several studies of children living in a restricted cultural environment and in recent studies of isolated mountain communities, such evidence was obtained. In the mountain communities it was found, for example, that below the age of approximately four or five, all children developed at apparently the same rate. It is well known that children below three or four all require approximately the same order of mental development in order to adjust to their surroundings. Above the age of approximately five, sharp differences were found in the intellectual development of children of different communities. In the more isolated communities the average intellectual attainment was found to be lower than in the less isolated communities.

In the study of four communities of various degrees of isolation it was found, for example, that the per cent of cases below average intelligence ranged from 84 to 25, decreasing in proportion with the decrease in isolation. Of significance was the finding that with age the intelligence quotients decreased rapidly in many cases, the decline being greater for children over ten than for children between six and ten.

It is probable that ordinarily in normal children cortical integration continues concomitantly with the development of a higher and higher order of conceptual mental activity. This integrative activity of the cortex may be assumed to diminish during adolescence and the mental development of the individual is henceforth mainly determined by the psychological processes involved in the learning mechanism.

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THIS NUMBER CONTAINS VOLUME TITLE PAGE AND CONTENTS

Vol. 12 No. 5 MAY, 1936 Serial No. 60

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EFFECTIVENESS OF TOKEN-REWARDS FOR CHIMPANZEES

BY
JOHN B. WOLFE
Yale Laboratories of Primate Biology

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EFFECTIVENESS OF TOKEN-REWARDS FOR CHIMPANZEES[1]

JOHN B. WOLFE

From Yale Laboratories of Primate Biology

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[1] This study was conducted while the author was a Fellow of the National Research Council working in the Yale Laboratories of Primate Biology. The work was done under the supervision of Doctor Robert M. Yerkes to whom the writer is greatly indebted for numerous suggestions and criticisms in connection with the work and for the generous provision of laboratory facilities. Thanks are further due to Doctor Henry W. Nissen for thoughtful counsel concerning the experiments, the control of subjects incident to experimentation, and the designing of apparatus. The data were collected in 1932–33 and 1933–34.

I. INTRODUCTION

Extensive investigations have been made since the turn of the century on the relative effectiveness of various rewards as learning-producing and as work-eliciting agencies. Notable among the rewards used have been food, water, sex objects, and freedom from noxious stimuli. In the main the rewards have been objects or situations for which animals exhibit, from the observer's point of view, unconditioned seeking or avoiding tendencies. Hence, they may be called primary rewards.

One important aspect of rewards or incentives, however, has received little experimental attention, namely, secondary rewards. By secondary rewards are meant objects, external to the organism, which through use have become associated with a primary reward such as food, which evoke striving behavior, and which can serve as agents in establishing or in eliciting a distinctive sequence of acts leading to the secondary rewards. It is the writer's contention that under certain conditions the elicitation of a previously established sequence of acts by means of an object associated with a primary reward is evidence that the object is a secondary reward. If an object, for example, which has previously been associated with food elicits a series of acts which have never before led to the object but have led to food, then the food-associated object has been established as a secondary reward.

The problems investigated in the present study fall into the category of secondary or surrogate rewards. Attempts were made to determine in an exploratory fashion the effectiveness of such rewards for chimpanzees after it was evident that the objects used were secondary rewards.

The particular objects used in this study were poker chips. It was felt that manipulatable and easily transportable objects such as poker chips would have certain advantages as surrogate rewards: they are especially advantageous in that they are small, compact, available in standard sizes and colors, and relatively indestructible; they can be used in a variety of ways in investigating complex behavior; they are objectively separable from the primary rewards; and they may be used conveniently in work with organisms of different species including the human, particularly the young and the feebleminded.

The experiments herein reported concerning the effectiveness of chips (hereafter designated as tokens or token-rewards) for chimpanzees may be grouped around four central problems. The first problem reported is that of determining the relative effectiveness of tokens and food in eliciting a work-task. Certain performances rewarded by tokens were compared with similar performances rewarded immediately by food similar in kind and amount to that for which the tokens might be exchanged. A work technique was used inasmuch as it permitted the systematic variation of rewards while the task remained constant.

The second group of experiments was designed to determine the influence of token-rewards upon the effectiveness of delayed food rewards. In learning experiments with rats, chickens and human beings, it has been shown that a reward loses much of its effectiveness if the giving of it be postponed for an interval of time following the execution of the rewarded act. On the assumption that the same relationship would hold for chimpanzees in a work situation, i.e., that a delayed food reward would be less effective in eliciting a work-task than would an immediate food reward, token-rewards were introduced in certain delayed primary reward situations and were not introduced in others. The effectiveness of the secondary reward would be displayed if the work were enhanced by the introduction of the object which could later be exchanged for food.

The third group of experiments was undertaken to investigate the chimpanzees' ability to discriminate between tokens having different exchange values. Tokens of certain colors and sizes were assigned particular reward values including food, water, and activity-privileges. After the subjects had received training in associating the tokens with their particular reward values, conditions were arranged to provide the subjects with specific drives or motives and then with opportunities to select and to use the tokens appropriate to those motives.

The final and fourth group of observations in this study was made upon the capacity of token-rewards to elicit competitive behavior in social situations. The animals when paired were presented with tokens which could be worked for, kept, or collected from the floor. These observations were made to determine whether or not tokens would elicit behavior similar to that elicited by food when given to groups of chimpanzees.

II. APPARATUS AND SUBJECTS

The apparatus used in these experiments consisted of two restraining cages, four automatic food-delivering machines, a water-vending device, two subsidiary cabinets, a work machine, and an assortment of tokens.

The main restraining cage was circular in form and all-metal in material. The arrangement of the framework which was covered with heavy wire netting may be seen in figure 3. The cage was 148 cm. in diameter and 103 cm. in height. Two grilles, through which the animals worked, were 90° apart. They were 30 cm. wide and 72 cm. high. Each was barred with two 1.25 cm. steel rods vertically placed. Wooden shutters were hinged outside the grilles and could be closed when the procedure so demanded. The smaller restraining cage, which was used in some of the experiments, was built of material similar to that of the main cage and was 94 cm. high, 81 cm. wide and 120 cm. long. One end of the cage was a grille made of 1.25 cm. steel rods horizontally placed.

The automatic food-delivering machines, or venders, were constructed so that the insertion of a token (poker chip) effected the release of a food-reward. The mechanisms were encased in white wooden cabinets built of paneled sides on a solid base and covered with two hinged lids. The only two features which were visible from the front of a vender were the metal food cup and the black slot into which the tokens might be inserted. The dimensions of the cabinets were as follows: height, 78 cm.; width, 38 cm.; length, 58 cm. Figures 1 and 2 show the internal design of a vender. The large drum, which carried the food, was 48 cm. in diameter and 8 cm. in thickness. On its circumference were twenty food compartments, each one of which was 8 cm. deep. The drum was wood covered with 22 gauge galvanized iron and was mounted on a shaft which ran in ball bearings. The drum itself turned in a trough, lined with galvanized iron, which terminated in a chute leading to the food cup. Motion of the drum was effected by a weight fastened to a wire wound about a smaller drum on the main shaft. A twenty-tooth steel ratchet wheel fastened to the small drum controlled the movement. Since the weight attached to the wire prevented backward motion, only one pawl was needed to regulate forward movement. A brass door-catch served as the pawl. This pawl was governed by a 110 volt, direct current solenoid.

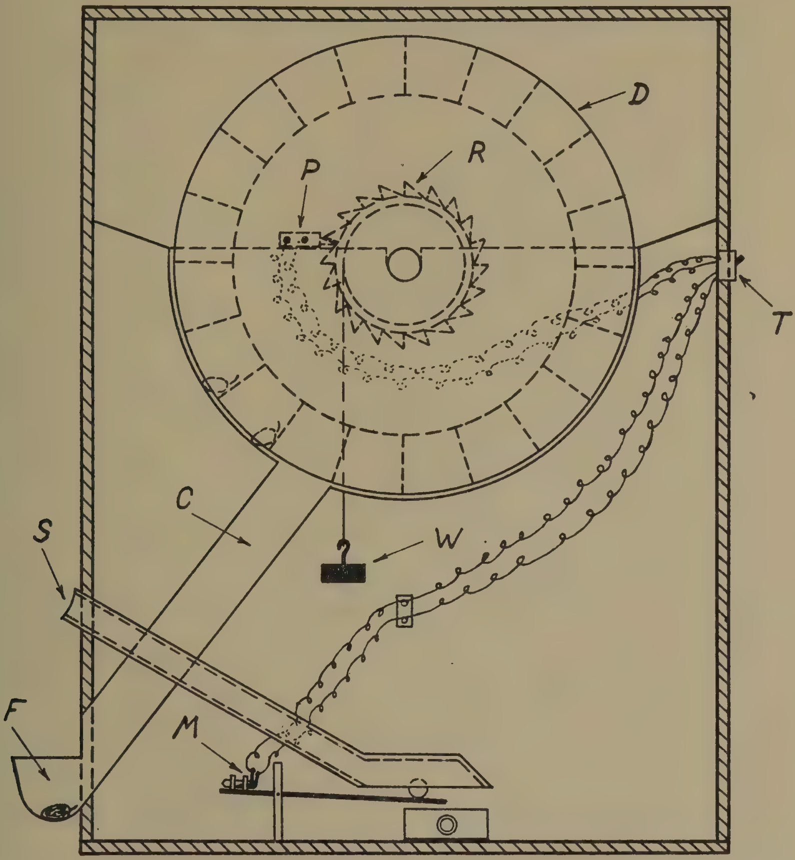

Fig. 1. Cross Sectional Diagram (Side View) of Food Vender Showing Internal Arrangement of the Mechanism

D, food drum; *C*, food chute; *F*, food cup; *S*, token slot; *M*, trigger switch; *T*, two-way toggle switch; *R*, ratchet wheel; *P*, electrically operated pawl; *W*, weight to effect movement of the food drum.

The mechanism for operating the large drum consisted of a wooden slot which conducted the tokens to a delicately balanced trigger. Mounted on the short end of this trigger was a glass-inclosed mercury switch which made contact only when the token was on the long end of the trigger. This contact was momentary, closing the circuit through the solenoid just long enough to draw the pawl and to allow one tooth on the ratchet wheel to pass. Thus the drum was permitted to turn through an angle of 18°,

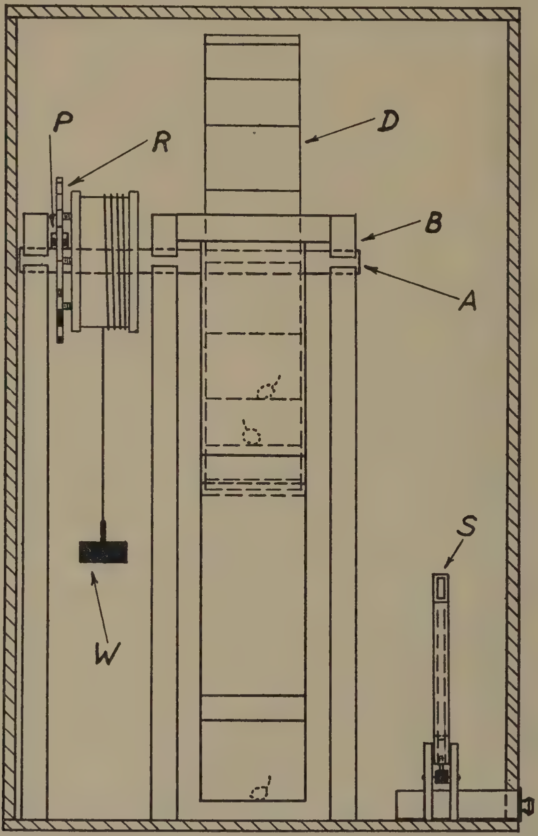

Fig. 2. Cross Sectional Diagram (End View) of Vender
D, food drum; *R*, ratchet on small drum; *W*, weight fastened to small drum to provide motion; *A*, main shaft to which small drum and food drum are attached; *B*, bearings in which main shaft turns; *P*, pawl; *S*, token slot.

a distance sufficient to discharge the contents of one food compartment into the chute. A small drawer just under the switch served to catch the tokens as they rolled off the trigger. The drawer was flush with the side of the cabinet and could be removed with a key for emptying.

A two-way toggle switch mounted on the back of the cabinet permitted an activation of the solenoid optional to the one involving tokens. By reversing the toggle switch the solenoid, and hence the vender, could be operated by a push button of the ordinary bell-ringing type from any place in the room.

The entire movable assembly could easily be taken out of the cabinet for cleaning. The venders were of sufficient strength and weight to withstand without damage the occasional pushes or pulls by the subjects.

The water-vending device consisted of a small white box, 10 cm. by 20 cm. by 25 cm., covered with an aluminum lid which opened automatically upon the closing of a push button switch by the experimenter. A water cup inside the box could be reached only when the lid was open.

The two subsidiary cabinets were used as receptacles for tokens which granted activity privileges. They were plain white boxes 78 cm. high, 19.5 cm. wide and 25 cm. long. Black slots similar to the ones on the venders were on the front, and drawers for receiving the tokens were in the bottom of each.

A weight-lifting device (fig. 3) was used as the work apparatus. It could be operated by the subject's extending its arm horizontally forward and moving a handle up through an arc of 90°. The handle was attached to two brass tubes which in turn were fastened by plain bearings to shafts on the two sides of an open wooden trough. Hence the tubes were free to move through an angle of 90°, or from a horizontal to a vertical position. The trough was 50 cm. long and 11 cm. wide. Each of the two tubes was composed of two parts, one of which fitted inside the other so that by means of a sliding collar and set screw it was possible to adjust the length to fit animals with varying reaches. The tubes were 1.5 cm. in diameter and were adjustable in length from 20 cm. to 35 cm. The difficulty of the task of lifting the handle was controlled by weights placed on a stem fastened by a bifurcated cord to the ends of the handle. The cord, below the point of bifurcation, passed across a pulley so that the weights swung free of the supporting framework.

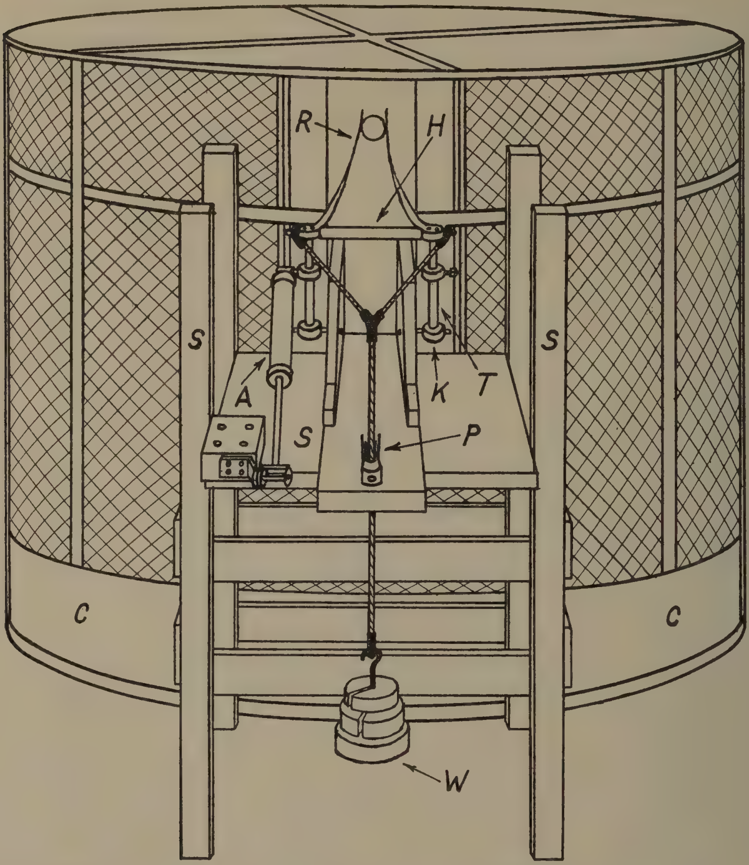

Fig. 3. Diagram of Work Apparatus and Restraining Cage
R, reward-holder; *H*, handle; *A*, air brake; *W*, weights; *K*, bearing; *P*, pulley; *T*, adjustable tubes; *S*, supporting frame work; *C*, restraining cage.

A spring-brass reward-holder was attached to the handle. The reward could not be reached by the animal until the handle had been lifted to a vertical position. A one-way air brake was connected to one of the brass tubes and served to let the handle fall back gradually to a horizontal position after the subject had released it. The supporting framework for the apparatus was adjustable in height to accommodate animals of different sizes. All moving parts of the apparatus were kept lubricated.

Composition poker chips of standard size, 3.75 cm. in diameter, and of one-half standard size were used for tokens throughout the experiments. The colors of the chips were red, green, yellow, dark blue, light blue, white, and black. Brass slugs, which were the same size as the large composition tokens, were also used.

Six immature chimpanzees, three males and three females, served as subjects. All were members of the New Haven experimental group of the Yale Laboratories of Primate Biology and are described in the laboratory records as follows:

TABLE 1

NUMBER	NAME	SEX	BIRTH DATE	AGE AT BEGINNING OF WORK
28	Alpha	Female	September 11, 1930	2 years 2 months
48	Bula	Female	April 27, 1930	2 years 5 months
26	Bimba	Female	Estimated, 1929	3 years, estimated
21	Bon	Male	Estimated, 1927	5 years, estimated
31	Velt	Male	Estimated, 1929	4 years, estimated
11	Moos	Male	Estimated, 1927	6 years, estimated

Alpha was born at the Anthropoid Experiment Station, Orange Park, Florida. Bula was born on the Abreu estate, Quinta Palatino, Havana, Cuba. The other subjects were from Africa. Alpha, Bula, Bimba, and Moos had been in the Yale Laboratories for over two years prior to the experimentation herein reported. Bon and Velt had been in the laboratories only a few months before the work began. With the exception of Moos, who had been used almost continuously for over two years in various studies, none of the subjects was well accustomed to experimentation.

III. GENERAL PREPARATORY TRAINING OF SUBJECTS

The general preparatory training of the subjects consisted of three parts: operation of the venders, discrimination between tokens with and without food value, and operation of the work apparatus. These will be considered in turn. Subsequent to or during the training, observations were made to determine whether or not the tokens functioned as secondary rewards.

A. Operation of venders

Before the problem of the effectiveness of token-rewards for chimpanzees could be attacked, it was necessary to establish in the animals an association between using tokens and getting food. To achieve that end white tokens and grapes were used. In order to get the grapes the tokens had to be inserted into a vender.

Procedure. The procedure which was used with success in training the subject to use the tokens to get food included three steps: (1) a period of orientation during which the animal was brought to the experimental room as many times as were necessary for it to gain confidence in the experimenter and to become thoroughly accustomed to the working quarters; (2) a period during which the experimenter continued to pick tokens up from the floor and insert them into a vender until the animal would reach into the food cup as soon as the experimenter started to place a token in the slot; (3) a period during which the subject came to insert the tokens. The manner in which the act of inserting the tokens was achieved varied from subject to subject.

Results. In table 2 a summary is presented as an introduction to the more complete description of the manner in which the individual subjects mastered the technique of getting food with the tokens. The individual descriptions follow the table. Since the procedures had to be adapted to the characteristics of the animals and consequently were not entirely uniform, the figures reported cannot be used for comparing the animals with each other.

Bon was allowed twenty sessions of approximately thirty minutes duration each for adjustment to the experimenter and to the experimental room before the tokens were introduced. When the tokens were presented, the subject would not take them either from the hand of the experimenter or from the floor. After forty tokens had been picked up from the floor and inserted into the vender by the experimenter, the subject began anticipating the appearance of the food by reaching into the food cup as soon as a token had been released in the slot and before the mechanism had had time to vend the food. Attempts to induce the subject to take the tokens in hand or to push them into the slot when they were balanced at the mouth of it failed, however, for nine experimental periods, or while 180 tokens were being inserted by the experimenter. At that point Bon began to put the tokens into the food cup and to hold his hand in anticipation of food. He very carefully took in succession seventeen tokens, which had been placed in the mouth of the slot after opportunity had been given him to pick them up from the floor, and dropped them into the food cup. Then the subject picked up a token from the floor and inserted it into the slot. A total of 237 tokens had been deposited by the experimenter before he executed this act.

TABLE 2

Showing for each subject the number of orientation sessions given (Step 1), the number of tokens inserted for demonstration into the vender before the food was anticipated (Step 2), and the total number of tokens inserted before the subject inserted a token independently (Step 3)

SUBJECT	STEP 1	STEP 2	STEP 3
Bon	20	40	237
Alpha	22	10	120
Bula	18	17	93
Bimba	1	4	10
Moos	0	1	1
Velt	3	25	35

Alpha at the end of twenty-two half-hour sessions in the experimental room seemed adjusted to the situation and ready for experimentation. When the tokens were then introduced, the subject after examining them with hand, mouth, and nose dropped them. At that point the experimenter began inserting them into the vender and the subject secured the vended food. The connection between the insertion of a token and the appearance of food became apparent to the animal after ten tokens had been used. Extensive verbal, gestural, and manual attempts in ensuing sessions to get the subject to insert the tokens proved ineffective. Finally the experimenter balanced a token in the mouth of the slot and Alpha pushed it in. This she did on twenty successive trials before she came finally to insert the tokens herself. Always before a token was balanced in the slot, the animal was given an opportunity to pick it up from the floor and insert it herself. Including the twenty tokens the subject had pushed in from the mouth of the slot, a total of 120 tokens had been used before the subject learned to insert them independently.

Bula required eighteen experimental sessions before adaptation to the experimental room was achieved. When tokens were placed on the floor near her following the adaptation sessions, she did not examine them in any way. After the experimenter had inserted seventeen tokens, the subject began to anticipate the appearance of the food as soon as a token was released in the slot. After four more tokens had been used, she began to push them in when they were balanced at the mouth of the slot by the experimenter; this she continued for eleven successive trials. She then made six unsuccessful attempts to insert a token which she had picked up from the floor. The failures were due in part to the hasty manner, almost a throwing movement, in which she tried to put the tokens into the slot. Her unsuccessful efforts were continued with decreasing frequency in the following ten experimental sessions during which time a total of twenty-two attempts were made. Then Alpha, who had previously learned to use the tokens, was brought into the experimental room so that Bula might see her use the tokens. After Alpha had used twenty tokens, Bula tried to insert one but was pushed away from the vender by Alpha. Alpha was then restrained by the experimenter, and Bula persisted in her attempts until she succeeded in inserting a token into the slot. Thereafter she had little difficulty with the task.

Velt was introduced to the tokens after three sessions in the experimental room. He initiated no attempts to inspect or to handle the tokens. Twenty-five were inserted into the vender by the experimenter before Velt began to anticipate the food by reaching into the cup as soon as a token had been released in the slot. When the experimenter began to hand him the tokens to insert, he dropped them on the floor immediately. However, he would push them into the slot if they were balanced at its mouth. This act he repeated ten times before he independently performed the complete series of acts leading from the picking up of the token to the securing of the food.

Bimba was given only one session for orientation. From the start she was accompanied by Alpha, a subject experienced in using the tokens. When the tokens were placed on the floor near the vender, Alpha began to insert them at once. Coincident with Alpha's insertion of the fifth token Bimba reached into the food cup ahead of Alpha but was crowded out by the latter before the food appeared. After Alpha had used a total of ten tokens, Bimba picked up one and attempted to insert it, but she was pushed away by Alpha who took the token. At that point Alpha was restrained, whereupon Bimba succeeded in inserting a token after she had dropped it four times. She subsequently had little difficulty in inserting tokens.

Moos was introduced to the experiment without his being given any sessions for orientation, since he had been used extensively in laboratory work and was acquainted with the experimenter. He examined the tokens which were on the floor but lost interest in them very quickly. Then the experimenter picked up a token, directed the subject's attention toward it, and inserted it into the vender. The subject took the reward from the food cup, ate it, and immediately picked up a token which with difficulty he inserted into the slot. He showed marked excitement when he obtained the food. After he had used ten tokens, he could insert them in one motion.

B. *Discrimination between tokens with and without exchange value*

Preparatory to the determination of whether or not the tokens actually were secondary rewards and prior to the determination of their effectiveness was compared with that of food in work and in other situations, the subjects were given opportunity to learn that white tokens were always exchangeable for food when inserted into a vender and that brass tokens were not. The importance of the establishment of such associations will be evident in the experiments on the effectiveness of tokens; it insured that the animal should attend, in a given situation, to the nature of the token before attempting to secure it.

Procedure. The procedure used in affording the animals an opportunity to associate white tokens with food and brass tokens with no reward consisted of two parts. In the first one the animals, while in the restraining cage, were presented with a choice-board containing a white token and a brass one. The former token when inserted into the vender procured a grape; the latter, nothing. Twenty choices were allowed per experimental session. The sessions were given on successive days. The criterion of success in discriminating between the two tokens was that the subjects select only white tokens during two successive experimental sessions. The sessions were continued for each animal until his performance met this criterion.

The second part of the procedure, which followed the successful termination of the first, consisted in presenting the animals with only brass or valueless tokens. The choice-board containing two brass tokens was placed before the animal in the restraining cage. If the animal inserted one of the tokens into the vender, another one was put in its place. The experimenter continued to supply the tokens until the animal no longer used them within a period of ten minutes. The procedure was discontinued after no brass tokens had been used in two consecutive sessions.

Results. The results obtained under the two experimental procedures are presented in table 3. The first two columns in the table present the data obtained when there was a choice for the animals between the white and the brass tokens. The third column in the table shows the number of brass tokens which were used when only brass ones were available. The subjects who used the brass tokens under this condition did so only in the first experimental session. It may be seen that the subjects very quickly learned to select only white tokens in the choice situation and to avoid taking brass tokens when only brass tokens were available.

Further results confirming the preceding evidence that the subjects were discriminating between the white and brass tokens were obtained with Alpha, Bimba, and Bula. Ten white and five brass tokens were tossed into a room of the chimpanzee living-quarters occupied by these three subjects together with Kambi, an animal not used in the token-reward experiments. Alpha, Bimba, and Bula immediately began to collect the white tokens. Alpha got four of them; Bimba, two; and Bula, four. Then Alpha took from Bimba's mouth the two which the latter had secured. Alpha had been observed to take food from Bimba's mouth in the same way. Bimba in turn grabbed one from Bula. Kambi, who had looked on for a moment when the tokens were first thrown into the room, picked up two of the brass ones. The only other chimpanzee who seemed to pay any attention to the brass tokens was Bula. After all the white tokens had been taken from the floor, she picked up a brass one but discarded it immediately. She kept her white ones, however, until they were recovered by the experimenter some five minutes later.

TABLE 3

Showing for each subject the number of experimental sessions of twenty trials each required to reach a learning criterion in the choice situation of white and brass tokens, the number of brass tokens chosen in those sessions, and the number of brass tokens used when only brass tokens were available

A white token obtained food. A brass token obtained nothing

SUBJECT	WHITE VS. BRASS CHOICE SITUATION		BRASS TOKEN SITUATION
	Number of sessions	Number of brass choices	Number of brass tokens used
Bon	3	1	0
Alpha	6	7	1
Bula	3	3	0
Velt	3	9	0
Moos	4	10	9
Bimba	3	5	0

An incidental observation was made on Bimba while she was receiving practice in using white tokens to get food from a vender prior to the introduction of the brass tokens. Just as a white token was extended toward her, she smacked her lips as if anticipating food. A grape was then extended toward her in the same way and the lip movements again occurred. Further observations were made of the anticipatory lip movements just after the subject had learned that brass tokens would not obtain food. The white tokens and the grapes would elicit the lip smacking but the brass tokens would not do so.

C. Operation of work apparatus

The use of a work-task in the main experiments on the effectiveness of tokens for chimpanzees necessitated preliminary training in operating the work apparatus. Subsequent to, or in the course of, this training tests were made to determine whether or not the tokens met the criteria of secondary rewards (p. 13).

Procedure. The procedure used in training the animals to operate the work apparatus was adapted to the characteristics of the individual subjects. The animals were placed in the restraining cage, with access to the work apparatus and a vender. During the learning of the task, grapes were placed in the reward-holder of the apparatus for all subjects except Moos. For him tokens were used. The experimenter assisted all of the subjects except Moos by gestures, verbal directions, and manual guidance. The reason that Moos was given no assistance will be stated in the discussion of his results.

The tests to determine whether or not the tokens which had been associated with food had reward value were made with five of the subjects after they had learned the task of operating the work apparatus with grapes in the reward-holder. The tests for these subjects consisted in placing a token in the reward-holder of the work apparatus to find out whether or not the token would elicit habits which would lead to the token and which had previously been formed with food as the incentive. In addition, tests were made to see whether or not the brass or valueless tokens would elicit the work-task. For the sixth subject, Moos, the test for reward value of the tokens consisted in using the tokens as incentives in the reward-holder during the learning of the work-task.

Results. With one exception the five subjects which were given assistance in learning the work-task mastered it very quickly. It will be recalled that grapes were used as incentives in the reward-holder for these subjects. Velt learned to execute the task in the first session; Bimba and Alpha, in the second session; and Bon, in the third session. Bula, however, required a longer time. She, for some reason, could not be induced to extend her arm along the trough of the work apparatus and grasp the handle until the eighteenth session. During the nineteenth session she executed the work-task while the experimenter assisted her by gestural and verbal directions. In the next session she performed the task without any assistance. After the subjects had learned to operate the work apparatus, food tokens were placed in it. The five animals immediately secured them. Brass or valueless tokens when placed in the reward-holder did not elicit the work-task. These results demonstrated that the tokens were secondary rewards in that they elicited a series of habitual acts which led to the tokens but which had not before led to them.

Moos learned to operate the work apparatus in a way somewhat different from that of the other subjects. He had learned to operate the vender almost instantly and had been very eager and alert in using tokens to get food. So it was felt that he could easily learn the operation of the work apparatus with tokens in the reward-holder as incentives and without the assistance of the experimenter. The tokens used were white ones which he had previously learned to use in getting food from a vender. His attention was called to a token as it was placed in the reward-holder of the apparatus. He looked toward it for a moment and then tried to get it by shaking and pulling the whole apparatus. This behavior was discouraged verbally by the experimenter. After a short pause, he began to manipulate the handle, trying to pull and to push it. Then he lifted it unskillfully and secured the token. Thereafter he experienced little difficulty in operating the work apparatus. He had learned the task in one trial.

The significance of the fact that a token was in the reward-holder when Moos learned to execute the work-task, aside from showing that the token was a secondary reward in that it elicited trial and error behavior which eventually led to the securing of the token, suggests that secondary rewards may be instrumental in producing learning. It should be emphasized that previous to this training Moos had neither operated the apparatus himself nor seen anyone else operate it. The token thus seemed to be a learning-producing agency. A final test of this would have been to extinguish the act without the subject's being allowed to use the token which he had secured through trial and error. This would have shown definitely whether or not an inedible object which had been associated with food had the capacity to produce learning. To have extinguished the work-response, however, would have been to interfere with the experiment at hand.

Comment on preliminary training. In view of the results presented it is now possible to state that tokens are practicable objects for use in experimentation with chimpanzees (1) because the animals learn readily to use them in obtaining food from a vender, (2) because they quickly learn to discriminate between tokens which will obtain food and tokens which will obtain nothing, and (3) because the tokens serve to elicit habits or acts not previously associated with them. The latter result together with observation of the striving behavior which the animals showed in the living quarters and of the anticipatory lip movements which one animal displayed when she was shown white tokens indicated that the tokens were secondary rewards.

IV. EFFECTIVENESS OF TOKENS AND FOOD IN ELICITING A WORK-TASK

As one approach to the determination of the effectiveness of food and token-rewards for chimpanzees a comparison was made of the extent to which the subjects would execute a work-task for a token-reward, on the one hand, and for a food-reward, on the other. Two measures of work performance were obtained. One was in terms of the amount of time required for the animals to do a fixed amount of work, a constant weight technique; the other was the amount of work, in pounds lifted, which the animals would do, a variable weight technique. In the former the unit of measurement was the time in seconds required for the animals to execute the work-task ten times. In the latter the unit of measurement was the maximum weight which the subjects would lift as determined by regularly increasing the weight until a point was reached beyond which they would not work. With both techniques the tokens could be used in obtaining food as soon as they were secured.

As apparatus, the circular restraining cage, the work machine, and a vender were used. The work machine and the vender were placed before the grilles of the restraining cage. White tokens and grapes were used as rewards. Bon, Moos, Bula, and Bimba served as subjects.

Each subject was given the same amount of practice in working for grapes and for tokens before regular experimentation began. During this practice, measurement was made of the time required by the animals to remove the two kinds of reward from the work apparatus. This was done because one subject in learning to operate the apparatus had, at first, exercised extreme caution in removing grapes. For this subject (Bon) practice was continued until the one reward was removed as quickly as the other. None of the other subjects showed consistent difference in speed of removing the two forms of reward from the holder.

A. Constant weight technique

Procedure. This experiment, which utilized the constant weight technique, consisted of eighty sessions for each subject. During forty of the sessions food was the incentive; during the other forty, tokens were used. In each session a subject was allowed to work for only ten units of reward in order to prevent fatigue and waning motivation.

The weights used in the work-task could be lifted by the animals without undue strain. For the three smaller subjects, Bon, Bula, and Bimba, the constant weight was 12 pounds. For Moos, the largest subject, it was 18 pounds.

The order of presentation of rewards was balanced. On any one day both kinds of reward were used. If grapes were the reward in the afternoon, they would be used again the following morning; then tokens would be used for two consecutive sessions, and so on to the end of the experiment. The reward-holder of the work apparatus was always loaded with the reward before the grille shutter was opened for the first trial of any experimental session. The next reward was placed in the holder the instant the handle fell back to a horizontal position, and so on to the end of the period.

Measurements of performance were in terms of time. When grapes were used as incentive in the work apparatus, the unit of measurement was the time required to execute the work-task ten times. When tokens were used as incentive, two time intervals were recorded. One was the total time spent per session in working for and in using ten tokens. The other was the total time required in exchanging the ten tokens for grapes. The ten intervals which composed the total time spent in using the tokens began at the instant the subject removed a token from the reward-holder and ended when it got the grape from the food cup of the vender. The difference between the total time spent in securing and in using the tokens and the time spent only in using the tokens was the measure of the animal's performance when tokens were the incentive. The data collected, then, consist primarily of the times, in seconds, required by each subject to secure comparable amounts of the two kinds of reward. The difference between these times indicates the relative effectiveness of the grapes and the tokens in eliciting the work-response. Stop watches served as timing instruments.

Results. Tables 4, 5, and 6 present a summary of the results for the four subjects. Interruptions due to temporary illnesses occurred for two of the subjects at the middle of the experiment. Bon was treated for intestinal parasites, and Bimba was allowed to rest for two weeks in order to recover from a cold. For these reasons the data from all subjects are divided into two parts which, for convenience of discussion, are called test data and retest data. For Bon and Bimba the test data consist of the records made before their illnesses. For the other two subjects, the test data were simply the records of the first half of the experiment. The retest data were in all cases the records of the second half of the experiment. Since the performances of Moos and Bula were not interrupted between the test and retest periods, it was possible to combine for each of them the data from the two periods in order to provide a sufficient number of measures to justify determinations of the significance of the differences between the token and the food data. The sigma scores which are based upon ten measures are presented merely to indicate trends. It should be emphasized, however, that each of the ten measures consisted of ten trials.

TABLE 4

Showing for each subject the average, variability, and difference scores of the time, in seconds, spent in working for grapes in the constant weight situation

Test period = 10 experimental sessions of 10 trials each
Retest period = 10 experimental sessions of 10 trials each
Combined = both the test and retest periods combined

SUBJECTS	PERIODS						
	Test		Retest		Difference of M's	Combined	
	M	σ	M	σ		M	σ
Bon	89.9	4.23	67.8	3.46	22.1	78.9	
Moos	58.2	4.87	55.0	5.15	3.2	56.6	5.23
Bula	69.9	7.16	68.7	5.37	1.2	69.3	6.36
Bimba	104.3	5.97	90.2	4.84	14.1	97.2	

TABLE 5

Showing for each subject the average, variability, and difference scores of the time, in seconds, spent in working for tokens in the constant weight situation

Test period = 10 experimental sessions of 10 trials each
Retest period = 10 experimental sessions of 10 trials each
Combined = both the test and retest periods combined

SUBJECTS	PERIODS						
	Test		Retest		Difference of M's	Combined	
	M	σ	M	σ		M	σ
Bon	90.8	4.38	69.1	4.95	21.7	80.0	
Moos	57.6	3.96	57.0	3.29	0.6	57.3	3.65
Bula	71.3	7.61	69.9	7.23	1.4	70.6	7.41
Bimba	114.6	11.63	106.2	8.30	8.4	110.4	

Tables 4 and 5 show the speed of working for grapes and for tokens, respectively. A rough indication of behavioral consistency is yielded by a comparison of the test and retest data. Table 4 shows that the average performances of Bon and Bimba in the test and the restest periods differed by 22.1 and 14.1 seconds, respectively, in the speed with which the animals worked for ten grapes. They both worked more rapidly in the second half of the experiment. Moos and Bula worked only a little faster in the last half of the experiment, the differences in the averages of the first and second half being for the two animals only 3.2 and 1.2 seconds, respectively. The variabilities of the subjects' performances as shown by the sigma scores were similar in the test and retest periods. When the test and retest data from Moos and Bula are combined, the variabilities do not increase materially.

TABLE 6

Showing for each subject the average, variability, difference, and significance of difference scores of the time, in seconds, spent in working for both grapes and tokens in the constant weight situation

Test period = 10 experimental sessions of 10 trials each
Retest period = 10 experimental sessions of 10 trials each
Combined = both the test and retest periods combined

SUBJECTS	PERIODS	REWARDS						D	$D/\sigma d$
		Grapes			Tokens				
		M	σ	σ_m	M	σ	σ_m		
Bon	Test	89.9	4.23		90.8	4.38		0.9	
	Retest	67.8	3.46		69.1	4.95		1.3	
	Combined	78.9			80.0			1.1	
Moos	Test	58.2	4.87		57.6	3.96		−0.6	
	Retest	55.0	5.15		57.0	3.29		2.0	
	Combined	56.6	5.26	1.21	57.3	3.65	0.84	0.7	0.48
Bula	Test	69.9	7.16		71.3	7.61		1.4	
	Retest	68.7	5.37		69.9	7.23		1.2	
	Combined	69.3	6.36	1.46	70.6	7.41	1.70	1.3	0.58
Bimba	Test	104.3	5.97		114.6	11.63		10.3	
	Retest	90.2	4.84		106.2	8.30		16.0	
	Combined	97.2			110.4			13.2	

The results obtained when the subjects were working for tokens (table 5) show for Bon and Bimba a marked increase in speed of working in the retest period over that of the test period. Moos and Bula worked at about the same rate in both of the periods. The differences, in seconds, in average speed of working in the test and retest periods were for Bon 21. 7, for Bimba 8.4, for Moos 0.6, and for Bula 1.4. The variability or sigma scores of the test and retest periods were remarkably constant for three of the subjects. For Bimba the variability was lower in the retest than in the test period, but it was relatively high in both periods. Little change in the variability scores for Moos and Bula occurred when the data from the test and retest periods were combined.

Consider, now, the differences between the grapes and the tokens as work-producing agencies. In table 6, parts of the data shown in tables 4 and 5 are presented and treated for purposes of such a comparison. The means of the combined measures show for three of the subjects negligible differences (1.1, 0.7, and 1.3 seconds) in speed of working for grapes and for tokens. The significance of the differences computed for two of the subjects, Moos and Bula, were 0.48 and 0.58 critical ratio units. For the fourth subject, Bimba, considerable difference was shown. She worked faster for grapes than she did for tokens. The average difference in the speed with which she worked for the two rewards was 13.2 seconds.

The differences between the average speed of working for grapes and that of working for tokens are all but one in the same direction when the periods of work are treated either separately or combined. The differences are in the direction of a greater time expended in securing the token-rewards. In addition, the extent of the differences between the speed of working for grapes and the speed of working for tokens which were found in the test period persisted in the retest period, except in the case of Moos. In the test period Moos worked faster for tokens by 0.6 second per ten trials while in the retest period he worked faster for grapes by 2.0 seconds per ten trials.

The variability of the performances, as expressed in standard deviations, was greater for three subjects when they were working for tokens than it was when they were working for grapes. Moos, to the contrary, showed greater variability when working for grapes during the test period, the retest period, and the two periods combined. This may have been due to the unusual stimulation which he appeared to derive from using the tokens to get food from the venders. When he first learned to use the tokens, he jumped about in the cage very excitedly, had an erection of the penis, and vocalized considerably. Thereafter, when using the tokens, he was noticeably more alert and anxious than were any of the other subjects.

B. Variable weight technique

Procedure. With the variable weight technique, in which the relative effectiveness of tokens and grapes in eliciting the work-task was measured in terms of the difference between the greatest number of pounds which the animals would lift for each form of reward, ten experimental sessions were devoted to each of the four subjects. Since considerable food was consumed per period and since the work done was strenuous, only one session was given per day. A session terminated when a subject would no longer work for either tokens or grapes. It was assumed that if an animal did not begin work within three minutes after a reward had been placed in the holder it was no longer interested in it.

The weights which the subjects were required to lift in getting the rewards were increased by steps of 2 pounds each from the starting point of 12 pounds. At any given weight, opportunities to secure both a token and a grape were given. Then the weight was increased, and again both rewards were introduced but in an order opposite to that used with the preceding weight, and so on until the animal quit working.

In order to establish whether or not an animal would lift more for one kind of reward than for the other, the following test was made. If an animal had secured one kind of reward at a given weight but had not got the other in the allotted time, then the task was increased in difficulty and both forms of reward were again used as lure. Now if the subject secured only the previously preferred reward again, it was considered to have worked harder for it than for the other form of reward. This criterion was adopted since the order of presenting the rewards might have made it appear that one form of reward was more effective in eliciting the work-task than the other. Suppose, for example, that the first reward presented with the 20-pound weight be a token and that the subject after securing it will work no further. It might be that the subject was fatigued or near satiation at that point and would have quit working no matter what the reward next to be presented was.

Results. The quantitative results are presented in table 7. Three of the subjects, Bon, Moos, and Bula, showed little difference in the weight which they would lift whether the reward was grapes or tokens. Bimba, on the other hand, rather consistently lifted more to get grapes than to get tokens. These findings are consistent with results obtained with the constant weight technique. It will be remembered that Bimba, there, worked faster for grapes than for tokens.

TABLE 7

Showing the greatest weights which the subjects lifted for each kind of reward (grapes and tokens) on ten different days and the difference between these weights

G and T represent grapes and tokens, respectively, and the numbers in the columns which they head represent in pounds the greatest weights lifted. The numbers under D are the differences between the two maximum weights lifted each day. The numbers preceded by the minus sign represent differences in favor of the tokens.

DAY	BON			MOOS			BULA			BIMBA		
	G	T	D	G	T	D	G	T	D	G	T	D
1	20	18	2	16	16	0	20	20	0	18	16	2
2	24	26	−2	20	20	0	22	20	2	26	22	4
3	26	26	0	20	20	0	24	20	4	28	24	4
4	26	26	0	22	22	0	20	22	−2	30	24	6
5	30	30	0	22	24	−2	26	26	0	30	26	4
6	34	32	2	24	24	0	32	30	2	30	30	0
7	36	36	0	22	22	0	28	26	2	26	24	2
8	36	34	2	22	22	0	30	30	0	32	30	2
9	34	34	0	22	20	2	24	26	−2	30	26	4
10	36	36	0	22	22	0	30	30	0	30	30	0

A consideration of the performances of the individual animals reveals that Bon on three occasions lifted a greater weight to get a grape than he did to get a token and that on one occasion the reverse was true. The differences in each case were only 2 pounds and may have been due to the order in which the rewards were presented as he never in any case continued to work until he met the criterion of harder-work which had been adopted. On each of these occasions he seemed to quit work because the weight was heavy rather than because a particular reward was unattractive.

Moos' general behavior in the form of attempts to lift the heavier than 22-pound weights did not suggest that he tried harder to get the one rather than the other kind of reward. That on one day he lifted 2 pounds more to get a token than he did to get a grape and that he did the opposite on a later day are probably insignificant since he did not continue to work for the given rewards until the criterion was met. It will be noted that the points, in pound weights, beyond which Moos did not work were not as great as they were in the cases of the other subjects. This was no reflection upon either his strength or his motivation. He was the largest subject in the experiment and no doubt could have lifted the heaviest weights, but the weight-stem of the apparatus was not sufficiently long to accommodate enough weights to test the maximum that he might have lifted. In view of this fact, to the apparatus was attached a restraining device which restricted considerably the use of the shoulder muscles in lifting the weights. This device reduced the size of the weight which he could lift because it made the act primarily one of arm movement.

On only one occasion did Bula meet the criterion of working harder to get grapes than to get tokens. That was in the third period when she secured two grapes by lifting heavier weights than she would for tokens. In order to test whether or not she was working to her maximum for grapes and for food-tokens, a light blue token, which she had previously learned to use in getting out of the experimental room and returning to the living quarters, was introduced on three occasions after she had stopped working for food and for food-tokens. These tests were made in the sixth, eighth and tenth sessions of the experiment. How Bula had learned to use the light blue token and under what conditions she used it will be told in a later section. Suffice it here to say that she became proficient at its use to the extent that it had to be out of her sight or she would not work for any other kind of reward. It should be emphasized that in these tests the blue token was placed in the reward-holder of the work apparatus only after the subject had quit working for the two regular rewards and also after the weight had been increased by 6 pounds. On all three occasions she pulled in the light blue token, stood before the door of the restraining cage until she was released, straightway inserted the tokens into the proper receptacle, and climbed upon the experimenter preparatory to leaving the room. She had not been lifting her maximum by at least 6 pounds to get the grapes and food-tokens.

Bimba met the criterion of working harder for one kind of reward than for the other in five of the ten periods. She lifted greater weights for grapes. In three of the remaining periods she lifted 2 pounds more for grapes than for tokens.

Additional experimental work was done with Bimba since she had demonstrated in the regular experimental periods that she would work harder, in general, for grapes than for tokens. Her work was extended until on each of five days she stopped working for the tokens before she did for the grapes. Then, following the usual three minute period in which she would not work for a token, more tokens were placed in the reward-holder. After four or five tokens had been added, she lifted the weight and secured the tokens. This suggests that the reward value of the tokens may be cumulative.

Summary of results with work techniques. Three of the subjects showed little difference in speed of working at a constant work-task whether the reward in the apparatus was food or tokens. The fourth subject worked faster for food. The variability of the performances of the subject which worked faster for food was greater when tokens were the incentive than when food was the incentive in the apparatus. The variability of performance of the other three subjects was not markedly different under the two conditions of reward; for two of these subjects the differences which did occur were in the direction of more variability for the tokens than for the food reward.

With the variable weight technique, it was found that three of the four subjects lifted on any given day about as much to get tokens as they did to get food. The fourth subject, on the other hand, rather consistently lifted greater weights for the food. These findings are consistent with those obtained with the constant weight technique. The subject who had worked faster for the food than for the tokens at the constant work-task also worked harder for the food than for the tokens under the variable weight procedure.

V. EFFECTIVENESS OF TOKENS IN DELAYED REWARD SITUATIONS

The experiment now to be described sought to ascertain the effect of tokens in situations wherein intervals of time were introduced between the execution of a work-task and the reception of a food-reward. Experiments in both maze-learning and discrimination situations have shown that as food-rewards are postponed for intervals of time which are progressively increased their effectiveness progressively decreases. On the assumption that the same thing would hold in work situations, that is, that food-rewards when postponed for various periods of time after the execution of a rewarded act would be less effective than immediate rewards as work-producing agencies, tokens were used in certain delayed reward situations and were not used in others in order to determine what influence they would have upon the effectiveness of delayed food-rewards in evoking a work-response.

Two techniques were used in the study. In one, the limited work technique, the subject could execute the work-task only once and then a period of delay was introduced before the food-reward was given. In the other, the unlimited work technique, the subject was free to execute the work-task as many times as it cared to in a fixed period of time, but food-reward was not given until the end of the period.

A. Limited work technique

Four experimental conditions were used with the limited work technique. (1) The subject was allowed to work for a token but was not permitted to use it in getting food from a vender until the end of a period of delay. The delays were increased trial by trial, beginning at zero, and the measure of the effectiveness of the rewards was taken in terms of the length of delay beyond which the subject would not work. (2) The subject was allowed to execute the work-task, after which act a period of delay was introduced before a food-reward was given at the vender. This condition differed from the first in that no tokens were involved at all; the subject simply had to lift the handle of the work apparatus and presently food appeared at the vender. Again, as in the following conditions, the measure of the effectiveness of the reward was taken in terms of the length of delay beyond which the subject would not work. (3) This condition was identical with the second except that five brass, or valueless, tokens were in the restraining cage throughout all the delays. The valueless tokens were introduced to provide something with which the subjects could occupy themselves during the delays just as in the first condition when they had had the food-tokens. (4) The subject was permitted to work for and to deposit a token immediately and was then required to wait until the food appeared at the end of the delay. This condition differed from the first in that the subject did not keep the tokens during the delays.

As apparatus the circular restraining cage, the work machine, and a vender were used. Shutters before the two grilles of the cage could be opened or closed as the experimental conditions demanded. Grapes were used as the food-reward in all conditions. Moos, Bimba, Bula, and Velt served as subjects. The weight lifted in the work-task was always the same for a given subject; for Bimba, Bula, and Velt, it was 12 pounds; for Moos, it was 18 pounds.

Procedure. The order in which the four experimental conditions were introduced was the same for each subject and corresponds to the sequence shown in the preceding section. The chimpanzees were familiarized with the acts involved in getting food under the particular condition before the delays were started. In each condition and with each subject eighty practice trials were given to insure the animals' familiarity with the procedure.

In all four conditions the order of increase of delay was the same. Until the delays reached one minute in length, the increase was five seconds per trial; from one minute to two minutes the increase was ten seconds per trial; from the two to three minute delays it was fifteen seconds per trial. Thereafter the delays, in order, were 3, 4, 5, 7, 10, 15, 20, 30, 45, and 60 minutes, and 1.5, 2, 3, 5, and 24 hours.

With delays over one hour it was not practicable to keep the animal in the experimental room throughout the entire period of delay. On such occasions the procedure was as follows: The subject was brought to the experimental room in the forenoon and was given opportunity to work for a token. Then after five minutes, leaving the token on the restraining cage floor, it was returned to the living quarters and was brought back to the experimental room five minutes before the end of the particular period of delay. The following trial was begun on the next experimental session when the procedure was repeated with the next longer delay. Since the experimental conditions necessarily had to be varied with delays beyond one hour, the results obtained under this variation are not comparable with those secured when the animals remained in the experimental room throughout the delay.

The procedure may be made explicit by a description of the routine followed for one experimental session with condition 1. The subject was placed in the restraining cage with both grille shutters closed. After a token was placed in the reward-holder of the work machine, the shutter before that apparatus was opened. A stop watch was used to time the interval which elapsed between the opening of the shutter and the beginning of the work on the part of the subject. As soon as the subject had secured the reward, another stop watch was started and at the end of the particular delay interval being used the shutter before the vender was opened and the token could be exchanged for a grape. The shutter before the work apparatus was always closed as soon as the animal had secured the token. After the food had been consumed, the apparatus was put into readiness for the next trial, and so on, until the subject stopped working, that is, until it failed to execute the work-task within five minutes after opportunity had been given. The final limit of delay beyond which a subject would not work was not recorded until three failures had occurred. The greatest delay attained was the measure recorded for a subject. Only one experimental session was given per day except when the delays were over one hour (two subjects, condition 1).

Results. In table 8 the results obtained for the four subjects are presented in summary. It may be seen that without exception the condition most favorable to work was the first, the one in which the animal secured a token, kept it during the interval of delay and finally exchanged it for food.[2] Little difference was shown in the performances under the other three conditions.

The results of the observations in condition 4 indicate that if the tokens are to be effective in eliciting the work-task the interval of time elapsing between the moment of their insertion into the vender and the reception of the food must not be great. The effectiveness of the tokens as work-producing agencies declined with extreme rapidity if the food did not follow within one minute after their insertion into the vender. The results under this and the other conditions are described in more detail in the following accounts of the behavior of the individual subjects.

Condition 1. Moos and Bimba, when allowed to keep the token during the delays, did not reach a point beyond which they refused to work. Moos continued to work after five delays of twenty-four hours each; Bimba, after ten delays of five hours each. During the delays shorter than one hour both of these subjects spent most of the time in toying with the token, picking it up, dropping it, putting it in the mouth, and the like. During the ten, fifteen, and twenty minute delays Bula whined and ran about in the cage as if frustrated. She did not work after the delay of twenty minutes was introduced. Velt did not work after one hour delay. Following his third refusal to work in successive sessions, the token was removed from the reward-holder and was replaced with a grape. The grape was immediately secured, but not the token which was then put back into the holder. The same procedure was repeated and Velt again worked for the grape but not for the token. This suggests that the animal appreciated the delay situation and that the delayed reward was not strong enough to elicit work.

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[2] There is a temporal variable which was not controlled in these observations, namely, the order in which the experimental conditions were introduced. However, there is little likelihood that it was responsible for the enormous difference in performance under conditions 1 and 2. It will be noted that for two subjects the work-response was not inhibited by the delays in condition 1. In addition, eighty practice trials, without delays, were allowed all subjects before each new condition was introduced. These practice trials should have mitigated any perseverative inhibitory effects.

None of the four subjects hesitated in beginning to work as the delays became longer. They worked for a token either immediately or not at all.

Condition 2. Moos, Bimba, and Bula gave similar results when working with no tokens involved. Moos quit after a three minute delay, Bimba, after a one minute and fifty second delay, and Bula, after a one minute and forty second delay. All three animals showed progressive hesitancy in beginning work as the delays became longer although it was slight for Moos and Bula. Velt continued to work until the delay was thirty minutes. There were two failures, however, before that point was reached, one at forty-five seconds, the other at three minutes. The reason Velt attained a greater period of delay than did the other subjects may have been due to a regurgitation habit which he began when the delay was three minutes.

TABLE 8

Showing the lengths of delay beyond which the subjects quit working under the four experimental conditions

Condition 1 = work for token, delay, insert token and get food
Condition 2 = work, delay, get food—no tokens involved
Condition 3 = work, delay, get food—valueless tokens in cage
Condition 4 = work for token, insert it, delay, get food

SUBJECTS	CONDITIONS			
	1	2	3	4
Moos	>1 hr.	3′ 00″	2′ 00″	1′ 50″
Bimba	>1 hr.	1′ 50″	50″	1′ 50″
Bula	$\frac{1}{3}$ hr.	1′ 40″	1′ 40″	30″
Velt	1 hr.	*30′ 00″	2′ 45″	2′ 30″

* Two failures to work occurred before this delay was reached, one at forty-five seconds and the other at three minutes.

Condition 3. The presence of brass (valueless) tokens in the restraining cage throughout all delays did not prolong the work for any subject. Moos and Bimba stopped working at a delay one minute less than the delays reached in condition 2. Bula quit work at the same delay reached in condition 2. Velt quit work at the two minute and forty-five second delay, a marked decrease from his performance in condition 2. He did not regurgitate during the delays as black pepper had been lightly sprinkled over the floor to prevent it. Only Moos and Bimba played with the brass tokens during the delays. As the delays became longer all the subjects began work more slowly.

Condition 4. When the subjects worked for a token, inserted it into the vender, and then waited until a delay interval ended before getting food, the results were very similar to those attained under condition 3. For all subjects the promptness with which work began decreased as the delay intervals increased. This hesitancy in beginning work was preceded by and coexistent with a hesitancy in inserting the tokens once they had been secured. Moos, Bimba, and Bula did not insert within five minutes the tokens which they had secured after the delay periods shown in table 8, condition 4. This fact suggests that the tokens had acquired incentive value over and above that of a tool to be used in getting food.

The behavior of Moos and Bimba when the delays were first introduced in condition 4 varied considerably from any which they had previously displayed. Moos, upon inserting the token into the vender, extended his hand into the food cup and waited a moment. No food appeared. He then grasped the vender, one hand on each side, and began to shake it. Bimba's reaction in the same situation was in contrast with that of Moos. She merely sat down, whimpering slightly, and looked toward the experimenter. In anthropomorphic terms, it seemed that both subjects considered something to be wrong, and that Moos, the older subject, sought to do something about it himself while Bimba simply looked to the experimenter for aid.

B. *Unlimited work technique*

Part I. A further study of the effectiveness of token-rewards for chimpanzees was made by again using delayed primary reward situations but with opportunity to execute the rewarded act, the work-task, any number of times within a fixed period of time. At the end of the period, food-reward was given in proportion to the amount of work that had been done.

Three situations were used. (1) Tokens were placed in the reward-holder, one at a time, but they could not be exchanged for grapes until the end of the period. (2) Grapes were placed in the reward-holder, one at a time, but they could not be eaten until the work period was over, as each time the weight was lifted the grape was tipped by the experimenter into a glass jar. (3) Nothing was in the reward-holder; at the end of the work period the subject was given a number of grapes equal to the number of times the weight had been lifted. The difference between the number of tokens secured per unit of time (1) and the number of times the work-task was executed in an equal interval of·time when no incentive was in the holder (3) was considered as due to the effect of the tokens on the performance. The difference between the number of tokens (1) and the number of grapes (2) secured in equal periods of time was taken to show the relative effectiveness of the two rewards.

Moos and Bimba were the subjects. The apparatus was the same as in the previous delayed reward experiment. The work-task was constant for each subject. For Moos it was 18 pounds. For Bimba it was 12 pounds.

To insure the subject's familiarity with the conditions involved, preliminary training was given in each of the three situations. The practice in a particular situation just preceded the regular experimentation in that sitution. In situation 1 the subjects were given fifty trials, each one of which consisted of securing a token, of waiting momentarily until the shutter before the vender was opened, and then of exchanging the token for food reward. Following this training the subjects were given successively five one-minute periods, one three-minute period, and one five-minute period in which to work for tokens. At the end of each one of these periods any tokens which had been obtained could be used in getting grapes from the vender. In situations 2 and 3 the preliminary training was identical with that of situation 1, except that the subjects were executing the work-task either when grapes were in the reward-holder, or when there was nothing in it.

The results of the preliminary training are shown in table 9. For each subject is given the number of times per period the work-task was executed in each of the three situations. Moos did more work in each case than did Bimba. Moos' best performance occurred when food-tokens were obtainable, situation 1.

Procedure. The three situations were introduced in the order in which they were described. In each situation Moos was given ten experimental sessions of ten minutes work each. Bimba was given ten sessions of ten minutes each in situation 1, two sessions of ten minutes each in situation 2, and five sessions of ten minutes each in situation 3. Her reactions in situation 2, when the grapes which she had pulled in were tipped into the glass jar by the experimenter, were so violent as to contra-indicate her continued use in the situation. In situation 3 work was discontinued after five sessions because the work-response had been extinguished.

TABLE 9

Showing the number of times the work-task was executed per period in the preliminary training for the unlimited work condition

SUBJECT	SITUATION	LENGTH OF PERIOD						
		One minute					Three minutes	Five minutes
		1st	2nd	3rd	4th	5th		
Moos	1	13	15	12	10	13	19	27
	2	8	9	7	8	8	20	25
	3	3	2	3	5	4	6	7
Bimba	1	3	2	2	3	2	4	5
	2	1	2	1	2	2	2	1
	3	2	2	1	3	1	2	3

Measurement of the performance in each situation was in terms of the number of times the work-task was executed. In order to indicate the form of work gradient under the various conditions of delayed reward, the number of times the task was performed during each successive minute of each work session was determined. The subject was free to work throughout each one of the ten minute sessions without interruption; the experimenter in counting the number of work-acts simply noted them minute by minute.

The manner in which an experimental session was conducted in situation 1 follows. The subject was placed in the restraining cage and the grille shutters were closed. After a token had been placed in the reward-holder of the work-apparatus, the shutter before that apparatus was opened and a stop watch was started. For ten minutes the subject was free to work for tokens, one at a time, at a self-determined rate. Then the shutter before the vender was opened and the subject could exchange the tokens obtained for grapes. After the tokens had been used, the experiment was over for the day. For situation 2, in which grapes were placed in the reward-holder, the procedure was identical with that of situation 1 except that the grapes as they were pulled in, one by one, were tipped by the experimenter into a glass jar and were given to the subject at the end of the period. The procedure in situation 3 varied from that in the other situations by the absence of an incentive in the work apparatus.

TABLE 10

Showing for Moos the frequency of work-task execution per minute in ten experimental sessions in each of the three situations of unlimited work

Situation 1 = working for tokens for ten minutes, then using them to get food.
Situation 2 = working for grapes for ten minutes, then eating the grapes.
Situation 3 = working for ten minutes, then getting food (no reward in the holder).

SITUATIONS	NUMBER OF TIMES WORK-TASK WAS DONE PER MINUTE										TOTAL
	1st	2nd	3rd	4th	5th	6th	7th	8th	9th	10th	
1	74	31	18	16	9	9	10	6	5	7	185
2	64	22	24	16	22	12	6	8	8	6	188
3	23	7	4	2	3	3	2	0	2	0	46

Results. The data for Moos are presented in tables 10, 11, 12, and 13, and in figure 4. In table 10 the results from the three experimental situations are summarized. This table shows the total number of times the work-task was executed per minute under each of the three conditions used. It may be seen that the tokens as incentives and the grapes as incentives in the work apparatus were effective to about the same extent and that both were more effective than the situation in which no incentive was present in the work apparatus.

In tables 11, 12, and 13 are given the number of times the work-task was executed per minute per session when tokens, grapes, and no reward were in the reward-holder, respectively. The per cents given in the bottom row of each table are the ratios of the total number of times the work-task was executed per minute (i.e., for all the sessions combined) to the entire number of times it was executed in a given situation (i.e., when all the ten sessions of ten minutes each are combined).

TABLE 11

Showing for Moos the number of times the work-task was executed per minute in ten experimental sessions of ten minutes each when tokens were used as incentives in the reward-holder of the work apparatus

WORK SESSION	MINUTES OF WORK										TOTAL
	1st	2nd	3rd	4th	5th	6th	7th	8th	9th	10th	
1	9	3	2	3	3	3	2	3	0	0	28
2	8	4	2	2	1	4	0	3	0	2	26
3	6	6	2	5	0	0	3	0	0	0	22
4	9	6	1	0	2	0	0	0	0	0	18
5	8	0	2	0	0	0	0	0	2	0	12
6	5	3	1	1	0	1	1	0	1	3	16
7	7	4	1	4	2	1	1	0	0	0	20
8	9	2	2	0	0	0	0	0	1	1	15
9	7	3	3	0	1	0	1	0	0	1	16
10	6	0	2	1	0	0	2	0	1	0	12
Total......	74	31	18	16	9	9	10	6	5	7	185
Per cent...	40.0	16.8	9.9	8.6	4.8	4.8	5.4	3.2	2.7	3.8	

It is evident from table 11 that as time passed during any experimental session the number of tokens secured per minute decreased. The most marked decrease occurred between the first and the second minutes of the work sessions. Thereafter the decrease was more gradual. There is a suggestion of another gradient in the amount of work done in successive experimental sessions; the subject secured more tokens during the first session than during any other and tended to secure less per session as the experiment progressed. Inversions occurred. The gradient, however, was very slight, as 42 per cent of the 185 tokens were secured during the last half of the experiment.

TABLE 12

Showing for Moos the number of times the work-task was executed per minute in ten experimental sessions of ten minutes each when grapes were used as incentives in the reward-holder of the work apparatus

WORK SESSION	MINUTES OF WORK										TOTAL
	1st	2nd	3rd	4th	5th	6th	7th	8th	9th	10th	
1	6	4	4	4	4	2	2	3	2	1	32
2	8	3	4	2	2	3	1	0	1	1	25
3	5	3	3	2	3	1	1	0	1	0	19
4	8	3	4	3	3	2	2	2	0	0	27
5	6	2	1	2	2	2	0	1	1	1	18
6	10	3	2	0	0	0	0	0	0	1	16
7	7	2	2	0	1	0	0	0	1	2	15
8	6	1	2	1	1	0	0	1	1	0	13
9	6	1	2	1	2	1	0	1	1	0	15
10	2	0	0	1	4	1	0	0	0	0	8
Total......	64	22	24	16	22	12	6	8	8	6	188
Per cent...	34.0	11.7	12.7	8.5	11.7	6.4	3.2	4.3	4.3	3.2	

TABLE 13

Showing for Moos the number of times the work-task was executed per minute in ten experimental sessions of ten minutes each when no incentives were used in reward-holder of the work apparatus

WORK SESSION	MINUTES OF WORK										TOTAL
	1st	2nd	3rd	4th	5th	6th	7th	8th	9th	10th	
1	6	2	1	0	0	1	0	0	0	0	10
2	4	1	0	1	0	0	0	0	1	0	7
3	2	0	1	1	0	0	0	0	0	0	5
4	3	0	1	0	0	0	1	0	0	0	5
5	1	0	1	0	1	0	0	0	0	0	3
6	3	0	0	0	0	0	1	0	0	0	4
7	2	0	0	0	0	1	0	0	0	0	3
8	1	0	1	0	1	0	0	0	1	0	4
9	0	1	0	0	0	1	0	0	0	0	2
10	1	2	0	0	0	0	0	0	0	0	3
Total......	23	7	4	2	3	3	2	0	2	0	46
Per cent...	50	15.2	8.7	4.3	6.5	6.5	4.3	0	4.3	0	

Moos' general behavior in situation 1 indicated that he appreciated the experimental conditions or restrictions and moreover "enjoyed" them. His behavior was characterized by marked alertness and activity. While he was not actually at work securing tokens, he played with those he had in his possession. He would scatter the tokens about the floor, pick them up, put them in his mouth, take them out again, drop them, etc., until the end of the period. It was very seldom that he played on the side of the cage opposite to the vender. During the first few experimental periods he put the tokens directly into his mouth after taking them from the reward-holder of the work apparatus. Later he merely knocked them from the holder directly into the cage and sometime during the period raked them over near the vender. Rarely was a token left beyond arm's reach of the vender by the time the work period was over.

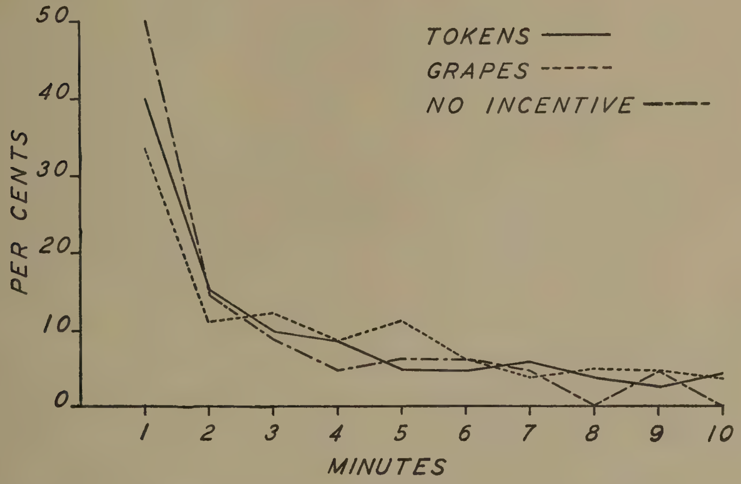

Fig. 4. Work Gradient: The Ratios (in Per Cents) of the Number of Times the Work-Task Was Executed per Minute for All the Sessions Combined to the Total Number of Times It Was Executed under a Given Condition of Reward

There were ten work sessions of ten minutes each under each work condition, i.e., with tokens, grapes, or no incentive in the reward-holder. (Data from tables 11, 12, and 13.)

Table 12 presents the amount of work which Moos did per minute when grapes were in the reward-holder. A definite gradient was shown in the amount of work done per minute as a session progressed. Also there was a slight gradient when the amount of work done per session is considered.

Moos showed a marked difference in behavior when he was working for grapes from that shown when he was working for tokens. In the sixth minute of the first experimental period when the animal was working for grapes, he had a temper tantrum during which he screamed, rolled on the floor, and covered his eyes with his hands when he glanced at the jar of grapes which he had pulled in but which he had not yet been permitted to eat. In each of the next two experimental periods he also had a violent tantrum. During the remainder of the sessions he usually stood at the work-apparatus, whining occasionally and, whether he was working or not, alternating in looking toward the jar of grapes and toward the reward in the holder of the apparatus.

Moos' rate of work in situation 3, with nothing in the reward-holder of the work-apparatus, is given in table 13. The subject worked more slowly in any given experimental session as it progressed. Also he worked slower, or less, in successive sessions until in the end the response was practically extinguished.

Moos' general behavior in situation 3 consisted of much walking around in the cage, considerable hesitation in executing the work-task and, as the experiment progressed, a lack of interest. During the first few sessions his reactions were about as follows: He would lift the weight, look toward the shutter which was in front of the vender, and, as it did not open, he would hold the handle up for several seconds before letting it fall again. Then after moving about in the cage for a while, he would again approach the work-apparatus, grasp the handle, look toward the shutter again, turn the handle loose, walk away, return and lift the weight, hold it momentarily, release it, move away, etc., until a session was over. In the last three sessions he was very "languid."

Graphical representations of the work gradient in the three situations are assembled in figure 4. The gradients shown are those of the frequency of work per minute, summated, in each ten experimental sessions. In all cases the greater part of the work was accomplished in the first two minutes of the sessions.

The results obtained with Bimba in situation 1 are presented in table 14. In each experimental session she soon quit working for the tokens. Of all the tokens secured in the experiment 85 per cent were got in the first two minutes of the sessions. After the fourth minute no tokens were secured in any session. The total number of tokens secured per session ranged from three to five, with four as the average. She did not work any more in the earlier sessions of the experiment than she did in those toward the end. From these data it appears that the subject was contented with a small number of tokens.

TABLE 14

Showing for Bimba the number of times the work-task was executed per minute in ten experimental sessions of ten minutes each when tokens were used as incentives in the reward-holder of the work apparatus

WORK SESSION	MINUTES OF WORK						TOTAL
	1st	2nd	3rd	4th	5th	6th to 10th	
1	3	0	0	0	0	0	3
2	1	1	0	1	0	0	3
3	3	1	1	1	0	0	6
4	4	0	1	0	0	0	5
5	2	1	1	0	0	0	4
6	3	0	1	0	0	0	4
7	2	2	0	0	0	0	4
8	3	0	0	0	0	0	3
9	3	2	0	0	0	0	5
10	2	1	0	0	0	0	3
Total......	26	8	4	2	0	0	40
Per cent...	65	20	10	5	0	0	

In situation 2, as has already been mentioned, Bimba reacted very adversely. When the two grapes which she had pulled in the first session were not given to her, she went into a temper tantrum and did not react kindly toward the experimenter when she was taken from the room. On the following day difficulty was experienced in bringing her to the experimental room, and once there she did not work at all. So she was given no further trials in the situation.

Bimba did not execute the work-task in situation 3 after the second session although she was given opportunity to do so on the three following days. In the first session she lifted the weight only twice: once in the first minute and once in the second. In the second session she lifted it once. A comparison of this behavior with that displayed in situation 1, shows that the tokens were instrumental in evoking the work-task in that the subject worked more extensively when they were present than she did when they were absent.

Part II. In the previous experiment it was shown that if a subject were free to work for ten minutes in a situation wherein one token at a time could be secured but not exchanged for food until the end of the session, the number of tokens secured per minute decreased as the time passed. This suggested the possibility that the number of tokens in a subject's possession might be one of the factors determining the gradient. To test this possibility, the two subjects which served in the previous experiment were given outright certain numbers of tokens and were then permitted to work for more of them within fixed periods of time.

Procedure. The experimental routine was identical with that of situation 1 in the previous experiment (see page 36) save that in the present instance the subject was given a definite number of tokens just before each work session began. These tokens, as well as those worked for during the ten-minute sessions, could not be used in getting food from the venders until the end of the period. With Moos determinations were made of the number of tokens that he would work for when he already had at the beginning of the period either five, fifteen, or thirty tokens. Five work periods of ten minutes each were given under each of these three conditions. With Bimba only one condition was used, that in which five tokens were given at the beginning of work.

Results. The results for Moos are presented in table 15 and in figure 5. The table shows for each of four conditions the number of tokens secured per minute in five work sessions of ten minutes each. In the first condition the subject was given no tokens before the work began (data taken from table 11 for purposes of comparison); in the second condition, five tokens; in the third, fifteen tokens; and in the fourth, thirty tokens. The numbers in

TABLE 15

Showing for Moos the number of tokens secured per minute during twenty experimental periods of ten minutes each

The subject had no tokens at the beginning of the first five work-periods; thereafter he had five, fifteen and thirty at the start of the second, third, and fourth groups of five work-periods, respectively. An 18-pound weight was used.

WORK PERIODS	NUMBER OF TOKENS SECURED PER MINUTE										TOTAL NUMBER OF TOKENS SECURED	PER CENT OF GRAND TOTAL SECURED UNDER 4 WORK CONDITIONS
	1st	2nd	3rd	4th	5th	6th	7th	8th	9th	10th		
1	9	3	2	3	3	3	2	3	0	0	28	
2	8	4	2	2	1	4	0	3	0	2	26	
3	6	6	2	5	0	0	3	0	0	0	22	
4	9	6	1	0	2	0	0	0	0	0	18	
5	8	0	2	0	0	0	0	0	2	0	12	
Sub-total.....	40	19	9	10	6	7	5	6	2	2	106	48.9
6	4	2	2	0	1	3	0	0	1	4	17	
7	4	0	0	1	1	1	0	0	1	1	9	
8	8	2	2	0	0	0	0	1	0	0	13	
9	4	2	0	1	3	0	0	1	0	2	13	
10	13	5	2	1	1	0	1	0	1	0	24	
Sub-total.....	33	11	6	3	6	4	1	2	3	7	76	35.2
11	2	1	0	1	0	0	1	0	1	0	6	
12	2	0	0	0	0	0	0	2	0	0	4	
13	1	0	0	0	0	1	0	0	0	0	2	
14	1	1	1	1	0	0	0	1	0	1	6	
15	0	1	0	0	0	0	0	2	0	0	3	
Sub-total.....	6	3	1	2	0	1	1	5	1	1	21	9.7
16	1	1	0	0	1	0	0	0	1	0	4	
17	1	1	0	0	0	0	0	0	0	0	2	
18	1	0	0	0	1	0	0	0	0	0	2	
19	0	0	0	1	0	0	1	0	0	0	2	
20	1	0	1	0	0	0	1	0	0	0	3	
Sub-total.....	4	2	1	1	2	0	2	0	1	0	13	6.2
Grand total..	83	35	17	16	14	12	9	13	7	10	216	100

the last column of the table are the ratios of the number of tokens secured under each condition to the total number secured under all conditions. It can be seen that the subject worked in proportion to the number of tokens he had in his possession at the beginning of the session. The more tokens he had, the fewer he worked for. This work, or "token-satiation" gradient is represented graphically in figure 5. The gradient is expressed in terms of the ratios of the number of tokens secured when the subject had in his possession none, five, fifteen, and thirty tokens to the total number of tokens secured under the four conditions.

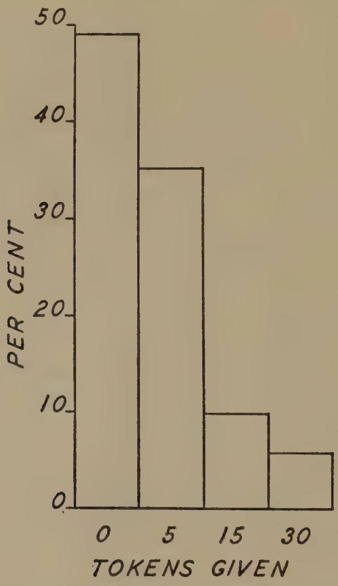

Fig. 5. Work Gradient: The Ratios (in Per Cents) of the Number of Tokens Secured from Work Apparatus under Conditions of the Subject's Possessing Either None, Five, Fifteen, or Thirty Tokens to the Total Number of Tokens Secured under the Four Conditions

There were five work sessions of ten minutes each under each condition of work. (Data from table 15.)

In the five sessions in which Bimba was given five tokens and then permitted to secure more by lifting the 12-pound weight she did not secure any. Her behavior in the previous delayed reward experiment suggested that she seemed satisfied with about four or five tokens and these results add to the significance of that suggestion. One factor, however, which might have influenced the results in this experiment was that she had just finished the delayed reward experiment in which she had reacted so violently to having the grapes which she had worked for tipped into the glass jar and not given to her until later. There might have been an emotional factor connected with working. However, when the five tokens were taken away from her and the shutter before the vender was opened, she worked for tokens when given opportunity to do so.

Summary of delayed reward experiments. The effectiveness of tokens as determined by the method of delayed reward may be summarized as follows. (1) Of the four conditions in the experiments with the limited work technique, the condition most favorable to work, that is, the condition which permitted the longest period of delay to be introduced between the execution of the work-task and the reception of the food-reward, was the one in which the subject secured a token, kept it during an interval of delay and finally exchanged it for food. Little difference was shown among the other three conditions in which the subjects either executed the work-task and waited until the end of a period for food, or executed the work-task and waited with valueless tokens in their presence until the end of the delay, or worked for a token, inserted it into a vender, and then waited for the food-reward. In the latter condition the effectiveness of the tokens as work-producing agencies declined markedly as the delays increased in length.

(2) Of the three situations in which the subjects could work for a period of time and receive from a vender at the end of the period food-reward in proportion to the amount of work done, the two situations most, and about equally favorable to work were those in which tokens and grapes were used as incentives in the work apparatus. The third situation which offered no incentive in the work apparatus was not very conducive to work.

(3) The number of tokens a subject had in his possession was one of the factors determining how many more tokens would be secured in a fixed period of time when none of the tokens could be exchanged for food until the end of the period. The more tokens possessed, the fewer tokens would the subjects work to secure.

VI. COMPLEX DISCRIMINATIONS INVOLVING TOKENS

A further investigation forming a part of the program for studying the effectiveness of token-rewards was a determination of the chimpanzees' ability to discriminate between tokens with different exchange values. Three discrimination situations were employed. In the first situation, tokens with different food values were presented. In the second one, tokens with food value and with water value were presented. In the third, tokens of activity-privilege values were presented. The problems attacked and the procedures employed will be described in connection with the several discrimination situations.

A. Discrimination between tokens of quantitatively different food values

The first problem was to determine whether or not the subjects could discriminate between two tokens of different visual characteristics when one of the tokens would obtain twice the amount of food that the other one would. Large grapes, as nearly uniform in size as it was possible to secure, were used. A dark blue token was assigned a reward value of two grapes; a white token, a value of one grape. Bon, Velt, and Alpha served as subjects in the experiment.

Procedure. Until the subjects had learned the discrimination, ten choices were given per experimental session. A choice consisted in taking from a choice-board either a white, a blue, or a brass (valueless) token. The brass tokens, which the subjects had previously learned not to take, were introduced so that the subjects would attend to the choice situation rather than reach blindly for a token. Only one vender was used, so that tokens of both colors had to be inserted into the same slot. If different slots had been used and if the tokens to be of value had to be inserted into specific slots, the discrimination might have been established on the basis of the slots rather than upon the basis of the amount of reward that followed the act of inserting a given token. The vender was activated by the experimenter who closed the switch either once or twice, depending upon whether a white or a blue token had been inserted.

The criterion of successful discrimination was that the subjects select the blue token first in ten successive choices. At the beginning of the experiment the subjects had had considerable experience in using the white tokens but had had none in using the blue ones. Hence it was expected that they would choose the white tokens first and might continue to do so unless steps were taken to introduce the blue ones into use. The following technique was employed. The white, the blue, and the brass tokens were presented together. If the subject chose the white one, the next choice was between a blue one and a brass one. If the subject then took the blue token from the two, the procedure was started over again with the original three tokens comprising the choice situation. In the treatment of the results a choice was considered to have been made only when opportunity was available to take one of the three tokens, i.e., it was not considered a choice when only the blue and the brass tokens were on the choice-board.

TABLE 16

Showing the number of times the blue tokens were chosen first in successive experimental sessions of ten choices each

The blue tokens could be exchanged for two grapes; the white tokens, for one grape; and the brass tokens, for nothing. The brass tokens were never chosen.

SUBJECT	SESSIONS OF TEN TRIALS EACH											
	1st	2nd	3rd	4th	5th	6th	7th	8th	9th	10th	11th	12th
Bon	0	0	3	8	10	10	10					
Velt	0	4	6	10	10	10						
Alpha	0	0	0	0	2	4	2	7	8	10	10	10

Results. The three subjects all met the criterion of successful discrimination within one hundred choices. The results are given in table 16. The number of times the more valuable token was selected first per ten choices is given for each subject in the table. The brass, or valueless tokens were never chosen.

B. *Discrimination between tokens of food value and of water value*

In a preliminary experiment it was found that each of two chimpanzees could use white tokens to obtain grapes from one vender, red tokens to get slices of oranges from a second vender, and blue tokens to get bananas from a third vender. The animals had learned each of the three acts at separate times before they were given opportunity to select a token from an assortment of the three kinds of tokens and to use it to get food. After making several errors in this choice situation, the subjects demonstrated convincingly that they could use any one of the tokens correctly to obtain food.

There was no control, however, in the experiment just described over the possibility that the animals were simply associating a particular token with a particular vender rather than with a particular food, or with a specific "need." It would be very difficult to establish whether an animal really seeks a grape at one time rather than a slice of orange. In order to determine whether or not a chimpanzee would choose tokens in harmony with his "wants" or inner processes, hunger and thirst were used since these two internal conditions could be varied relatively independently. If, when the chimpanzee were thirsty, he should persistently select the water-tokens, a relationship between known internal conditions and the use of the tokens would be established. The experiment now to be described was an attempt to find out whether or not such a relationship could be demonstrated.

Alpha, Bimba, and Velt were used in a preliminary attack upon the problem of whether or not the tokens would be utilized in harmony with known conditions of hunger and thirst. In this preliminary work there were indications that the hunger and thirst under the prevailing conditions of food and water deprivation were not actually dissociated, or, if they were dissociated, that the privations were not sufficient to make the dissociation obvious. Since these three subjects were being used by other investigators in the laboratory, it was not practicable to extend the periods of food and water deprivation beyond sixteen hours, i.e., the period between the late afternoon feeding and a late breakfast.

Fortunately, opportunity was available to observe two normal adolescent chimpanzees which were being used by Dr. C. F.

Jacobsen and the writer in an analysis of the functions of the frontal association areas.[3] These two animals, Becky and Lucy, were used for more intensive study of the relationship between hunger and thirst and the utilization of food- and water-tokens. The presentation of the results obtained with these subjects will follow a summary of the preliminary work with Alpha, Bimba, and Velt.

Procedure and results with Alpha, Bimba, and Velt. Before the subjects were given the critical trials in the choice and use of food- and water-tokens, each received training in the use of black tokens to get peanuts and of yellow tokens to get water. During this training as well as during the critical trials, the drive was controlled to the extent that for a known number of hours previous to experimentation the subjects at one time had been deprived of water but had been given an abundance of dry food, and vice versa at another time. The hunger in the training series resulted from a sixteen-hour food deprivation and the thirst from a sixteen-hour water deprivation. Likewise, in the critical trials of the experiment, deprivations of sixteen hours were used. Dry food, such as roasted peanuts and chimcrackers, were used during the period of these tests. The apparatus employed was a food-vender with an attachment on the side to vend water also. The two kinds of tokens had to be inserted into the same slot since, as previously mentioned, association between a particular token and a particular vender was a complication to be avoided. When a black token was inserted, the experimenter released two peanuts; when a yellow token was used the experimenter closed an electric switch which opened a lid, making available a cup containing approximately one-half gill of water.

In training an animal on the use of the tokens opportunity was given to choose between a brass and a black token, presented on a choice-board, if he had been deprived of food, or between a brass and a yellow token if he had been deprived of water. The amount of this training depended upon the number of trials required by each subject to meet the criterion indicating that an association had been formed between tokens and their individual reward-values. This criterion was that the animal immediately reach for the appropriate reward after he had inserted the appropriate token. That is, he must reach for the food as soon as he had inserted the black token into the slot of the vender, and he must reach for the water cup as soon as he had inserted the yellow token. In this training Alpha used seventy black tokens and sixty yellow tokens. Bimba used thirty black tokens and twenty-eight yellow tokens. Velt used each kind of token thirty times. Only one experimental session was conducted per day. The subjects seldom used as many as six yellow tokens per session; even though they had been without water for sixteen hours they usually quit working after four or five trials. Ten trials per session were allowed with the black tokens. The subjects did not seem to like the peanuts as much as they did the grapes which had been used as rewards in previous experiments.

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[3] A preliminary report of these analyses has been made. See Jacobsen, Carlyle F., Wolfe, J. B., and Jackson, T. A., An experimental analysis of the functions of the frontal association areas in primates. Journal of Nervous and Mental Disease, Vol. 82, No. 1, July, 1935.

In the critical trials the subjects were brought to the experimental room while either hungry or thirsty and were given opportunity to choose either the black (food) tokens or the yellow (water) tokens. Five choices were allowed per session. The order in which the drive was varied and the results of the subjects' choices are shown in table 17. An examination shows that no one of the subjects clearly demonstrated that the tokens were being selected solely on the basis of hunger or thirst. More food tokens were chosen, however, when the animals were supposedly hungry than when thirsty, and vice versa.

A fact which indicated that deprivation of food and water had not been sufficiently extended was that more frequently than not in any given session both kinds of rewards would be consumed. This led to the use of longer deprivation periods with Becky and Lucy.

Procedure and results with Becky and Lucy. The procedure used with Becky and Lucy differed in three essential details from that used with the other subjects whose data have just been presented. (1) The deprivations of food or water were for periods of twenty-four hours instead of sixteen. (2) One hour prior to each experimental session the subjects were allowed to eat peanuts and bananas to satiety if the drive under investigation were thirst, or to drink to satiety if the drive under investigation were hunger. (3) At the beginning of each series of critical tests, two food tokens and two water tokens were presented one at a time to determine first whether the supposedly satiated drive had really been satiated and second whether such satiation had operated to remove the alternative drive. Thus it was found on some occasions that satiation of hunger by feeding fifteen to eighteen bananas within half an hour not only removed the hunger drive

TABLE 17

Showing choice of tokens exchangeable for food or water under conditions of a sixteen-hour deprivation of food or water

Black tokens could be exchanged for food; yellow tokens, for water. B represents the choice of a black token; Y, the choice of a yellow token.

SUBJECT	SESSION	FOOD DEPRIVATION						SESSION	WATER DEPRIVATION					
		Trials					Sum of B-choices		Trials					Sum of Y-choices
		1st	2nd	3rd	4th	5th			1st	2nd	3rd	4th	5th	
Velt	1	B	B	Y	B	Y	3	2	Y	B	Y	Y	B	3
	4	B	Y	B	B	Y	3	3	B	B	Y	Y	Y	3
	5	Y	B	B	B	B	4	6	B	Y	B	B	Y	2
	8	B	B	Y	Y	B	3	7	Y	B	Y	Y	B	3
	9	B	B	B	Y	B	4	10	Y	Y	B	Y	B	3
	12	B	B	Y	B	Y	3	11	Y	Y	Y	B	Y	4
Bimba	1	B	B	B	B	B	5	2	B	B	B	B	Y	4
	4	B	B	B	B	B	5	3	B	B	Y	B	Y	2
	5	B	B	B	B	Y	4	6	Y	B	Y	Y	B	3
	8	B	B	Y	B	B	4	7	Y	B	Y	B	Y	3
	9	Y	B	B	B	B	4	10	Y	Y	B	Y	Y	4
	12	Y	B	B	B	Y	3	11	B	Y	Y	B	Y	3
Alpha	1	Y	B	B	B	B	4	2	Y	Y	Y	Y	Y	5
	4	B	B	B	B	Y	4	3	Y	B	Y	B	Y	3
	5	Y	B	B	Y	B	3	6	B	Y	Y	B	Y	3
	8	B	B	Y	Y	Y	2	7	B	Y	B	Y	Y	3
	9	B	Y	B	B	Y	3	10	Y	Y	B	Y	B	3
	12	B	B	Y	B	Y	3	11	Y	Y	Y	B	B	3

but apparently distressed the animal sufficiently to cause it to refuse water in spite of the previous privation.

Before the critical tests were administered, the subjects were given practice in using white tokens so that they might become acquainted with the operation of the water-vending device. Becky received sixty practice trials in using the white tokens to get water when only white tokens were presented. Lucy received forty-five practice trials in using the white tokens. Experience in getting food with red tokens had already been acquired.

TABLE 18

Showing for Lucy and Becky the choices of tokens exchangeable for food and water under conditions of a twenty-four-hour deprivation of food or water

The numbers in italics indicate choices not in harmony with the drive.

SESSION	BECKY				LUCY			
	Drive	Choices	Food	Water	Drive	Choices	Food	Water
1	Thirst	10	*10*	0	Thirst	10	*4*	6
2	Thirst	10	*1*	9	Thirst	10	*4*	6
3	Thirst	10	0	10	Thirst	10	0	10
4	Hunger	10	10	0	Hunger	10	9	*1*
5	Hunger	10	10	0	Thirst	20	*20*	0
6	Thirst	10	0	10	Thirst	20	*9*	11
7	Thirst	10	0	10	Thirst	10	0	10
8	Hunger	10	10	0	Hunger	10	2	*8*
9	Thirst	10	0	10	Hunger	10	10	0
10	Hunger	10	9	*1*	Thirst	10	*5*	5
11	Thirst	10	0	10	Thirst	10	*5*	5
12	Hunger	11	10	*1**	Thirst	10	0	10
13					Hunger	10	10	0

* The error was made blindly, i.e., the subject was not looking toward the choice-board when the token was picked up.

The results of the critical tests are summarized in table 18. It may be seen that Becky very clearly demonstrated her ability to use the tokens in harmony with her drive. To a slightly less extent, Lucy selected the tokens appropriate to her drive. In making the transition from one drive to the other, Lucy showed a tendency to select tokens similar to those she had used in the immediately preceding session.

Summarizing the results from the observations on the utilization of tokens in harmony with hunger and thirst drives, it may be said that three subjects with sixteen hours deprivation of food or of water did not show a dissociation of the drives, but that two subjects with twenty-four hour deprivation came to select the tokens in harmony with presumptive needs.

C. Discrimination between tokens of different activity values

As another step in the determination of the extent to which tokens could be utilized by chimpanzees to attain ends, certain tokens were assigned different activity-privilege values. The associations between the designated tokens and their activity-privilege values were established in the animals, and later the subjects were given opportunities to utilize these tokens in achieving definite ends.

Two activity situations were used: (1) leaving the experimental room and being returned to the living cage and (2) playing with the experimenter. A light blue token when inserted into a given slot attained the former; a small yellow token when inserted into another definite slot, spatially separated from the first, attained the latter.

Bula, Bimba, Alpha, and Bon served as subjects. Bon, however, had to be excluded from part of the experiment for reasons to be given later.

Procedure. Before observations could be made on the usage of the activity tokens, it was necessary to establish in the subjects an association between the acts of selecting and inserting the tokens and the activities which followed these acts. The technique employed in teaching the subjects that the light blue token might be used in effecting removal from the experimental room was to require that the token be inserted into the slot of a cabinet near the door of the room just before the subjects were taken to the living quarters after cessations of experimental sessions. The value of the play tokens was taught by having the subjects insert yellow tokens into a cabinet which was always in the same place on one side of the room and by following this act with play between the experimenter and the animal.

During the observations Bula, Bimba, and Alpha were, unless special experimental conditions prevented it, free in the experimental room. Bon was always on leash except when he was in the restraining cage. This fact limited to some extent the observations that could be made on his reactions in the experiment. He was not allowed to use the yellow tokens after his first trial since on that occasion he played too roughly, if his behavior could be termed play. Bula was by far the most adept of all the subjects in these experimental situations and, as a consequence, could be observed more frequently than could the other subjects.

After the associations between the tokens and their activity privileges had been established, the animals were provided various opportunities at different times to use the tokens in attaining appropriate goals. The adaptations of the general procedure, both in learning the value of and in utilizing the tokens later, which had necessarily to be made for the individual subjects, accompany the following accounts of the results.

Results. (1) Leaving experimental room. Bula, with the aid and insistence of the experimenter, inserted the light blue token in the slot on each of the first three times it was introduced. In each case, as had been her custom when leaving the experimental room, she tried to climb upon the experimenter as soon as he had gone near the door of the room. She was not permitted to do so, however, until the token had been inserted. The next three times the token was presented Bula inserted it without any aid from the experimenter, except that the token had been placed just in front of the proper receptacle. On the seventh and eighth times, the token was tossed onto the floor at a distance of about three yards from the slot into which it had to be inserted. Bula retrieved it, inserted it into the slot, and then turned around and jumped upon the back of the experimenter. The next two times the token was introduced the situation differed only in that the token was placed on the floor with an assortment of white (grape) and brass tokens. In each instance the blue token was selected and used appropriately.

Additional training in the use of the blue token was given after each of the following fifteen experimental sessions, and the results indicated that Bula had learned that the blue token had to be inserted into a slot before she was taken from the experimental room. Each time the experimenter stood in different positions in the room and the blue tokens were presented at different places in the room, always accompanied by the white and the brass tokens. Only twice did Bula fail to select the blue token; once she took a white token and once, a brass one. In the case of each error she was not allowed to leave the room until it had been corrected. The error in using the brass token was probably due to the fact that it had previously been placed partially on the top of the blue token in the hope that it—the brass token—might be used and hence make it evident to the subject that only the blue token could be used in securing release from the room.

In order to determine whether or not Bula would use the token in conditions which to the experimenter seemed to demand its use if its value were appreciated, three special situations were employed. The first situation consisted in isolating in the living quarters a chimpanzee to which Bula had a strong attachment. The isolation caused the chimpanzee to vocalize loudly. Similar vocalizations had, on previous occasions, caused Bula to quit work. In the present situation Bula was released in the experimental room with white and brass tokens scattered about the floor. Bula looked over the tokens as if she were seeking the blue one. Then the experimenter secretly placed the blue token on the floor. A few moments later Bula picked it up, inserted it into the proper slot, and climbed upon the experimenter, assuming the position used in going to and from the living quarters. The same situation was arranged on the following day and again Bula did nothing but look about the floor until the blue token was discovered.

The second situation which provided a motive for Bula's leaving the experimental room was not planned in advance. A photographer had been engaged to make a demonstration film of the subject at work. After the camera and lights had been arranged, the subject was brought into the room and released. She vocalized slightly and began striking at the photographer. This behavior was stopped by the experimenter who then made attempts to induce her to use white tokens in getting grapes from a vender. The attempts were futile. So the light blue token, with a number of white and brass ones, was placed on the floor. Bula at once grasped the blue token, inserted it in the correct slot and climbed upon the experimenter. The experimenter carried her out of the room but returned with her a moment later. She became angry and screamed until she had slight throat convulsions. This behavior seemed to indicate that she did not "wish" to be in the room.

Another situation which made the experimental room unattractive to Bula was provided by the introduction of a white rat. Bula at a previous time had been taken into a room in which a white rat was on a table. She had pulled the experimenter by the hand toward the door, thus indicating her dislike for the rat. The rat was produced in the experimental room at a moment when Bula was using white tokens to get grapes. She immediately quit using the white tokens, got the blue token from a box in which she had previously found it, and straightway inserted it in the proper slot. These tests indicate definitely that this subject used the blue token to get out of the room.

Bimba was required to insert the light blue token in the cabinet near the door of the experimental room until she would perform the act of her own accord. After the tenth time the token had been inserted, she performed the act without aid from the experimenter. Ten more trials were then given to strengthen the association between the token and the act of leaving the room. An incidental observation in point was made during the learning of the use of the "escape"-token. Bimba's regular work at the time was lifting weights to get food and white tokens. After the work was over, she was forced to use the blue token. On the fifth day for some reason she did not come to the experimenter when he opened her living room door preparatory to taking her to the experimental room, and it was only with difficulty that she was finally induced to leave the living quarters. Once in the experimental room, she was put in the restraining cage and a white token was placed in the reward-holder of the work apparatus. She immediately secured it but instead of inserting it into the food vender, as was her custom, she pushed against the cage door.

The experimenter quickly opened the door and Bimba took the token to the cabinet which on the four previous days had served as a receptacle for the light blue token and inserted it therein. This behavior suggests that she had learned that to put a token into a particular slot would effect her release from the room, but that she had not yet learned that it must be a light blue token.

Two situations were arranged to determine whether or not Bimba would use the blue token to get out of the room. In the first she was taken to the experimental room while her breakfast was being prepared and while the other animals in the colony were vocalizing as they usually did just prior to mealtime. Bimba resented leaving the living quarters, and as soon as she arrived in the experimental room she selected the blue token from an assortment of white and brass tokens and inserted it into the correct slot. She then climbed upon the experimenter's back and was returned to her breakfast. The other situation was provided by the experimenter's leaving the room while Bimba was engaged in using white tokens to get grapes from a vender. She was given twenty tokens and after she had begun to use them the experimenter left the room. She whined and then screamed. The experimenter reëntered the room and placed the blue token in the reward-holder of the work apparatus. Bimba secured it, although she had in her presence several white tokens, and, when the cage door was opened, used it appropriately.

Alpha and Bon did not give convincing evidence that they were using the blue token to gain its particular exchange value. This fact is probably associated with the observed disinclination of these animals to leave the experimental room. Their marked willingness to remain in the room, in contrast to the eagerness to leave the room shown by Bimba and Bula when their work sessions were over, probably was due to the temperamental characteristics of Alpha and to the fact that Bon was and had been in isolation from other subjects for a year. Alpha seemed content just to sit on the floor after an experimental session was over. These reasons made the forming of an association between using the blue tokens and leaving the room very difficult. After the subjects had used the blue token before leaving the room on forty occasions, a test was given to see if it would be used appropriately. The test situation was effected by striking a radiator with a mallet while the subject's attention was elsewhere. Neither subject showed any tendency to get the blue token, although both were startled by the noise to the extent that they worked no more in that session. It is possible that the startle was not sufficient to make the subjects "wish" to leave the room. A more likely account of their behavior, however, would be that neither animal had for lack of appropriate motivation formed an association between the blue token and escape from the room.

(2) Play activity. The observations on utilization of the small yellow tokens (play) are not easy to interpret inasmuch as artificial situations arousing in the subjects a desire to play were not readily available. However, the way in which at least two of the subjects behaved, both before and after inserting the tokens, indicated that a connection had been established between using the tokens and engaging in play activity.

The technique which was followed demanded that the subjects insert the tokens in a cabinet which was always located at the same place in the room. The insertion of the yellow token was always followed by attempts of the experimenter to initiate play with the animals. The number of tokens used in any session depended upon the enthusiasm with which the subject would play. As the training progressed, the experimenter took less initiative in the play; the subjects were allowed to dominate the activity if they would.

Bula, on the first day of training, inserted a token at the experimenter's "request" but did not respond to the play attempts. In the following seven sessions she played enthusiastically after the insertion of each of sixteen tokens. Then, over a period of six sessions, she selected thirteen yellow tokens from an assortment of yellow and brass ones and with one exception played vigorously after each token had been inserted. The play was a sort of "tag" game in which she would tackle the experimenter and then scamper away. In the next experimental session Bula was allowed to use white tokens in getting grapes until she was satiated. Then white, yellow and brass tokens were placed on the floor. Bula selected a yellow token, inserted it, and came running toward the experimenter. As the experimenter moved away, she tackled him as she had done in the play on previous days. On the following day the procedure was repeated with very similar results. It seems reasonable to believe that the animal associated the token with play activity.

The training of Bimba differed from that given Bula in that the form of play consisted in the experimenter's swinging the animal. After twenty-five tokens had been used over a period of fourteen sessions, Bimba, with arms uplifted, came of her own accord toward the experimenter and engaged in the play. When opportunity was given in the next session for her to insert the yellow tokens without insistence by the experimenter, she did not do so. Neither did she use these tokens appropriately in any of the following ten sessions when opportunity was given. However, after being directed to insert a yellow token she would prepare to play, albeit unenthusiastically at times. It may be inferred that she knew that the insertion of the token was followed by play, but she never of her own accord inserted it in order to play.

Alpha's reactions to the play situation were disappointing and inconclusive. She never, after any of the twenty-five times that she was directed to insert the yellow token, made any move to play until the experimenter had sat down on the floor and extended his arms toward her. Then she seemed perfectly contented to sit quietly in his lap. This lack of a willingness to play in the experimental room was strange. In the living quarters the animal would play enthusiastically with the experimenter even to the extent of jumping into his arms from a high perch.

Summary of results of discrimination experiments. In the discrimination situations (1) all of the subjects learned to select tokens which would procure two grapes rather than tokens which would procure one grape, (2) two subjects with pronounced hunger and thirst drives selected tokens appropriate to each need, and (3) some of the subjects associated tokens with activity-privileges. Observations indicated that the subjects who did not choose tokens leading to activity-privileges did not at the time have drives appropriate to the activities selected.

VII. OBSERVATIONS OF SOCIAL BEHAVIOR WITH RESPECT TO TOKENS

It has long been known that when food is given to a group of chimpanzees in a cage a competitive element enters into gaining possession of and keeping the food. Stronger or older animals often take food from the less strong or younger ones. In some cases the more timid animals will not take food until the more dominant ones have collected what they will and have begun to consume it. In order to determine whether or not similar behavior would occur with respect to tokens, the observations now to be described were made in social situations with tokens present.

Four different situations were used. In the first, pairs of subjects were confined in the large restraining cage and definite numbers of tokens were tossed into the cage. The tokens could not be used in getting food until the end of a fixed period of time. In the second situation the pairs of subjects were placed in the restraining cage and opportunity to work for tokens was given. Only one subject could work at a time, and a token could be used as soon as it was secured. In the third situation pairs of subjects were put in the restraining cage and a number of tokens given outright to one or the other member of the pair. As the tokens could not be used for five minutes, opportunity to keep them or to take them, as the case might be, was provided. In the fourth situation, one subject of a pair was confined in a cage with access to a vender while the other subject was confined in an adjoining cage without access to a vender. A grill was between the two cages. Tokens were given to the subject which was without access to a vender and observations were made on the ensuing behavior.

A. Rivalry in collecting free tokens

Three pairs of subjects were used in the experiment, Bimba and Bula, Velt and Bula, and Moos and Velt. Bimba and Bula were observed in thirteen successive sessions; Velt and Bula, and Moos and Velt, in five sessions each. In any session the subjects were allowed to remain in the restraining cage for about three minutes before ten tokens were tossed on the floor between them. The shutter before the vender was kept closed until five minutes after the tokens had been introduced; then it was opened and the subjects were allowed to use the tokens.

The number of tokens possessed by each subject at the moment the shutter was opened each session is given in table 19. It will be remembered that Bimba and Bula were young females; Velt, a male some months older; and Moos, a male about two years older than Velt.

Observation when the tokens were introduced showed fairly consistent behavior on the part of the subjects of a given pair throughout the sessions in which they were together. When Bula was with Bimba, the former usually waited until the latter had picked up several tokens before she obtained any herself. In each of three sessions Bimba picked up nine tokens; Bula whined upon each of these occasions and extended her arm toward Bimba as if she were trying to obtain additional tokens. Bimba handed her one token in one of the sessions and two tokens in another. During the five-minute periods there was very little activity on the part of the subjects. After these periods were over, Bimba was always first in exchanging her tokens for food. Incidentally, on four occasions while she was so engaged Bula begged for food, i.e., whimpered and extended her hand toward the food which Bimba had secured. The food being vended was unpeeled orange slices, and when the begging occurred Bimba gave Bula the peels.

TABLE 19

SUBJECT	SESSION													TOTAL
	1	2	3	4	5	6	7	8	9	10	11	12	13	
Bimba	8	7	4	6	7	7	7	7	4	7	7	6	7	84
Bula	2	3	6	4	3	3	3	3	6	3	3	4	3	46
Velt	9	10	9	9	7									44
Bula	1	0	1	1	3									6
Moos	10	10	10	10	10									50
Velt	0	0	0	0	0									0

Bula was even less aggressive when she was paired with Velt than when paired with Bimba. She always waited for Velt to pick up his tokens first; and, when the periods were over and after Velt had used his tokens, she, at a look from Velt, dropped her token or tokens on the floor. Velt then used them in getting food. Bula did not beg for either tokens or food while paired with Velt. During the course of these observations Velt and Bula were cage mates in the living quarters. Frequently at lunch time Bula had waited to take her food until Velt had got his share. Also she had been noticed to drop part of her food after Velt had finished eating what he had been given. On such occasions Velt had picked up and had eaten the food dropped by Bula. The similarity between this behavior with respect to food and the reactions to tokens in the experimental sessions is striking.

Moos was entirely dominant in the sessions in which he was paired with Velt. On the first day when the tokens were introduced, Velt picked up one token; Moos very deliberately reached over and took it from Velt's hand. In the remainder of the sessions Velt did not again pick up a token, nor did he get any of the food when the five-minute periods were completed. Some weeks prior to these observations Velt and Moos had been caged together in the living quarters, but had subsequently been separated due to the rough treatment which Moos had given Velt.

B. *Rivalry in working for tokens*

Another situation arranged to afford opportunity for rivalry with respect to tokens consisted in presenting a token in the reward-holder of the work apparatus when a pair of subjects were in the restraining cage. If the tokens were capable of eliciting rivalry in this situation, such should be shown in the subjects' attempts to gain the position before the work apparatus. Five experimental sessions of working for tokens were given to the three pairs of subjects. The tokens were made available in this fashion: when the attention of both subjects of a pair had been obtained, a token was placed in the reward-holder of the work apparatus. After the token had been secured and exchanged for food, a second token, again with both subjects looking on, was placed in the reward-holder, and so on until the end of the session. Ten tokens were used per session.

The observations disclosed results very similar to those obtained in the free token situation. Bimba crowded or pushed Bula away from the work apparatus in the first three sessions so that the latter subject got only one token. In the two remaining sessions, however, Bula got four and five tokens, respectively; she became more aggressive and resisted Bimba's attempts to push her away from the work apparatus. When paired with Velt, Bula made no attempts to work for the tokens, and Velt, in turn, did no work when paired with Moos. So again it may be said that the tokens served as stimuli to competitive activity.

C. Taking tokens from another subject

Six tokens were handed by the experimenter to one or the other of the subjects in a pair, and then a five minute delay was imposed before the tokens could be exchanged for food. Observations were made on Bimba and Bula on five occasions when the six tokens were given to Bimba and on five occasions when they were given to Bula. When Velt and Bula and when Moos and Velt were together, each subject was given the tokens three times.

During the observations of Bimba and Bula, Bimba succeeded in getting nine tokens of the total of thirty which were given to Bula. Bula got ten of Bimba's thirty tokens. The manner in which Bula got the tokens from Bimba was by whining and extending her hand, palm up, toward Bimba. This begging behavior on two occasions ceased after one token had been given her, twice after two tokens had been given her, and once after four tokens had been received. Bimba did not beg for the tokens. She would wrestle very playfully with Bula and, when opportunity presented itself, take a token. It appeared to the experimenter that for Bimba taking the tokens was secondary in importance to playing. In three of the periods Bimba secured only one token from Bula; in the fourth and fifth periods she obtained two and four tokens, respectively.

When Velt was paired with Bula, he secured all of her tokens each time and in no instance did he let her have any of his. She watched him very closely, but she did no begging. Velt did not take Bula's tokens all at once. After getting three or four, he would wait until the end of the five-minute period, use them, and then start toward Bula. She would drop one token at a time and move away. This behavior was similar to that frequently observed in the living quarters with respect to food. Velt, after eating his food would start toward Bula, and the latter would then drop a part of her food and move to some other place in the room.

Moos dominated the situation entirely when he was with Velt. He kept the tokens which were handed to him and took those which were handed to Velt. Velt took the six tokens from the experimenter only once. Thereafter he paid no attention to the experimenter's attempts to give him the tokens. So on the occasions when it was his turn to take the tokens, they were tossed onto the floor. Moos obtained them all.

It is of interest to note that the two animals of a given pair showed a fairly consistent relationship to each other with respect to obtaining tokens in the three foregoing social situations.

D. Sharing tokens

In the previous experiments Bula displayed what has been termed begging behavior in the company of Bimba when Bimba was given all the tokens. More extended observations of the phenomenon were made with the two subjects when one of them at a time had access to a vender. This condition was arranged by placing two restraining cages together with only a grille separating them. Before a second grille of one of the cages a vender was placed. The subject in this latter cage thus had access to the vender while the animal in the other cage did not. Tokens were given to the subject which did not have access to the vender.

During the first five sessions Bula was the subject with access to the vender. In the first session when Bimba was handed a token she played with it for four minutes before Bula, who sat at the grille watching, made any attempts to get it. Suddenly Bula extended her hand through the grille toward Bimba, made "beckoning" motions, and then vocalized (a kind of whine). Bimba promptly handed her the token and Bula immediately exchanged it for food which she herself ate. The procedure was repeated five times with results differing from those of the first trial only in that the begging began almost as soon as Bimba had been given a token. Just as the sixth token had been used by Bula, a chimpanzee in the living quarters began to scream. Bula became excited, vocalized slightly, and stood listening with hair erect. At that point Bimba was handed another token. When within one minute Bula had not made the slightest effort to get it, it was taken from Bimba by the experimenter and the light blue token, which Bula had formerly associated with leaving the experimental room, put in its place. Bula at once began to whine and motion to Bimba. Bimba gave her the token. Bula took it to the door of her cage and began to whine. When the cage door was opened, she went directly to the cabinet near the door of the experimental room and inserted the token. Then she ran to the experimenter and climbed on his back. It will be remembered that Bula had previously used the light blue token in a situation which differed from the present one only in that she had worked to get the token rather than begged to get it. In the next three sessions Bula got thirty tokens from Bimba by continuing the begging. Bula got food with each one of the tokens while Bimba got nothing. In order to see if the begging would persist when the animal was not hungry, Bula was brought to the experimental room on each of two days immediately after she had been given bananas until she would eat no more. She was again given access to the vender and a token was handed to Bimba. On neither day did Bula make any attempts to get the tokens within the ten minutes allowed. The satiation had taken away the effectiveness of the tokens in eliciting the begging behavior.

The observations which were made in five sessions while Bimba had access to the vender failed to disclose any begging. Bimba would watch Bula play with the tokens and occasonally would grab for one when Bula was near the grille which separated them, but she did not react otherwise toward the tokens.

Summary of social observations. Results of observations made when tokens were introduced into social situations affording opportunity for competitve behavior show that the tokens elicited rivalry or competition (1) in the free token situation, (2) in the work situation, (3) and in the situation in which a number of tokens was given directly to the one or the other animal of a pair. For one subject, the tokens elicited begging behavior.

VIII. DISCUSSION

It seems reasonable to believe this study shows that at least some of the problems of secondary rewards and secondary motivation are subject to concise attack by the method and techniques herein used. The findings give evidence that it is possible (1) to investigate the laws governing the establishing and functioning of secondary rewards and (2) to use secondary rewards as a means of analyzing certain primary drives. In the present experiments the chimpanzees fairly rapidly came to respond to the tokens in a manner similar to their way of responding to primary goals. The tokens, after they had been used a few times by the animals in getting food from a vender, aroused acts or habits which had never before been associated with the tokens and compared favorably with food in eliciting various performances.[4]

It is striking that three out of four subjects under the conditions both of the constant weight technique and of the variable weight technique in the work situation showed little difference in performance whether the incentives were grapes or tokens which could be exchanged immediately for grapes. Mention should be made, however, that in the constant weight situation there was consistency in direction of differences. The means and the variability of the work data tended to be greater for tokens than for food. The reason for the non-conforming results of Bimba, the fourth subject, is unknown. The fact that she had a slight cold may have influenced her motivation, and a change in motivation may influence the relative effectiveness of the two incentives. With very weak or very strong motivation, for example, the secondary reward may be with reference to the primary reward much less effective than when the drive is medium in strength. This hypothesis is in harmony with results obtained by Szymanski[5] from white rats provided certain assumptions be granted. Szymanski, varying the intensity of the intraorganic stimulus (the drive) while keeping the incentive constant, found that rats with a weak hunger drive would make an imperfect performance even though previously, when more hungry, they had made a perfect performance. Let us regard Szymanski's maze as a manipulandum, a behavior support, a physical object to be run-through in getting food. Now, if the tokens in our work be regarded as objects to be manipulated in seeking food, then, we should expect a weak drive to manifest itself in the reactions to the tokens.

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[4] Williams conducted a study with white rats which has bearing on the problem of secondary or conditioned rewards and how they operate. She found that a white compartment which in a discrimination situation served as the food box was effective as a reward in the subsequent learning of a maze. Equally important was her finding that the white compartment rapidly decreased in its reward value in the maze situation even though it was still used as the food box in the discrimination situation. It would be valuable to know whether or not tokens would continue to evoke a series of responses when the tokens themselves are never subsequently exchanged for a primary reward but when other similar tokens are given such usage in a different place and at a different time.

Williams, Katherine A. The reward value of a conditioned stimulus. Univ. Calif. Pub. in Psychol., 1929, *4*, No. 3, 31–55.

The results obtained on the effectiveness of tokens, or secondary rewards, in the delayed reward situations have several implications. It will be remembered that the condition most favorable to the elicitation of a single work-act was (1) the one in which the subject secured a token, kept it during an interval of delay, and finally exchanged it for food. Little difference was shown among the other three conditions, in which the subjects (2) executed the work-task and waited until the end of a period for food, (3) executed the work-task and waited with the valueless tokens in their presence until the end of a delay, or (4) worked for a token, inserted it into a vender, and then waited for the food reward. A comparison of the results attained under conditions 1 and 2 shows that the secondary rewards were effective in that they increased the extent of delay between the act of lifting the weight and the receiving of the primary reward at the vender. An attempt to analyze this effectiveness leads to a consideration of the results attained under the other conditions of delay.

The results from condition 4 showed that the tokens lost their effectiveness when there was a delay of about two minutes between insertion of the token and reception of food. This fact seems comparable with results which various investigators have found in the case of the effectiveness of delayed primary rewards, and comparable with our results under condition 2.[6] This can hold, however, only if the act of inserting the secondary reward into the vender in this case be considered comparable with the acts which others have used preceding the introduction of a delay in obtaining the primary rewards.

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[5] Szymanski, J. S. Ein experimenteller Beitrag zur Analyse der bei Entstehung neuer Gewohnheiten mitwirkenden Faktoren. Pflüger's Arch. f. d. ges. Physiol., 1918, *170*, 197–220.

Now in condition 1 there was no delay between the insertion of the token and the reception of food. The possession of the token by the subject during the delay between securing the token and inserting it into the vender might have been the factor which made condition 1 most favorable to work. Why should the possession of a valuable token during the delay be effective? Since the token through association had become connected with food, it might have served as an attention-maintaining mechanism, that is, it might have served constantly to *reinstate* more or less effectively the past usage to which the tokens had been put. Just any attention-keeping mechanism was not effective in prolonging the delays, as shown by the use of the valueless tokens in condition 3. It may have been that the presence of the food-associated token prevented the animal from discovering that there was a delay between the execution of the work-task and the final getting of food. Further analytical study is necessary before conclusions may be drawn as to what is basic in this matter.

When the subjects were allowed to set their own pace at working during a fixed period of time and receive food in the end in proportion to the amount of work done, grapes and tokens were about equally effective when used as incentives in the work apparatus. With no reward in the work apparatus, little work was done. In these conditions the work gradient was negatively accelerated. It is likely that this gradient was a function of (1) the number of tokens in the subject's possession and (2) the limited time during which the subject could work. Our results on the first point showed that in a fixed period of time an animal will work in proportion to the number of tokens in his possession. The more tokens he has the fewer will he work for. In connection with the second point, the effect of unlimited time can only be conjectured, as all of our experiments dealt with work periods of fixed duration. With unlimited time in which to do a fixed amount of work one might expect on the basis of the goal gradient hypothesis that the work rate would be positively accelerated in that the more tokens the subject had secured the nearer he would be to his primary goal, food.[7]

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[6] For references, see: Wolfe, J. B. The effect of delayed reward upon learning in the white rat. J. Comp. Psychol., 1934, *17*, 1–21.

That the subjects learned to select tokens which had twice the reward value of other tokens is in harmony with previous experiments on the influence of amount of incentive on performance. Nissen and Elder showed that for chimpanzees in delayed response situations an increase in the amount of incentive used consistently increased the delay "limits" and accuracy of performance.[8] Grindley found that chicks fed six grains of rice per trial learned to find food at the end of a pathway faster than did chicks fed only one grain of rice.[9]

The selection of tokens in harmony with hunger and thirst drives shows that the tokens are feasible objects for use in analysis of the interrelationships of different drives. The results obtained on this secondary incentive level are somewhat comparable to those of Hull and Leeper who worked with a lower form of animal on a primary incentive level. Hull[10] and Leeper[11] both found that rats could set up and utilize habits on the basis of hunger and thirst, i.e., the differentiating cues were internal. Closely connected with the utilization of tokens in harmony with hunger and thirst drives is the work on the association of tokens with certain activity-privileges. The animals, when their motivation in the judgment of the experimenter appeared adequate to the particular situation, quickly formed associations between tokens and activities.

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[7] Hull, C. L. The goal gradient hypothesis and maze learning. Psychol. Rev., 1932, *39*, 25–43.

[8] Nissen, H. W. and Elder, J. H. The influence of amount of incentive on delayed response performances of chimpanzees. J. Genet. Psychol., 1935, *47*, 49–72.

[9] Grindley, G. C. Experiments on the influence of the amount of reward on learning in young chickens. Brit. J. Psychol. (Gen. Sec.), 1929, *20*, 173–180.

[10] Hull, C. L. Differential habituation to internal stimuli in the albino rat. J. Comp. Psychol., 1933, *16*, 255–273.

[11] Leeper, R. The rôle of motivation in learning: a study of the phenomenon of differential motivational control of the utilization of habits, J. Genet. Psychol., 1935, *46*, 3–40.

There are a number of ways of characterizing a token (poker chip) which has through use become associated with a primary reward. It may be considered as: (1) a sign or symbol of something to come or happen, e.g., food, water, or an activity-privilege; (2) an instrument, a tool, a means to an end, a manipulandum; (3) something which, because of certain past associations, now has intrinsic value. One is unable to choose between these possibilities from the present experiments. To regard a token as a sign or symbol (1) seems justifiable provided a distinction is made between a physical object and a language process or a pure stimulus act. But symbolism has so many different connotations that its use is confusing.[12] The second and third characterizations seem preferable.

IX. SUMMARY

1. This experimental investigation was concerned with (*a*) a determination of whether or not poker chips, or tokens, could serve as surrogate or secondary rewards for chimpanzees and (*b*) a determination of the relative effectiveness of such tokens, once they were established as secondary rewards, in comparison with that of a primary reward, food.

2. The observations were grouped around four central problems: (*a*) the effectiveness of tokens as work-producing agencies; (*b*) their influence upon the effectiveness of delayed food-rewards; (*c*) their effectiveness as tools in attaining ends in harmony with specific drives or needs; (*d*) their effectiveness in eliciting competitive behavior in social situations.

3. The experiments made use of restraining cages, food-vending machines, a water-vending device, subsidiary cabinets as

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[12] Morris, C. W. The concept of the symbol. J. Phil., 1927, *24*, (I) 253–262, (II) 281–291.

token receptacles, a work machine, and an assortment of poker chips. Six chimpanzees, three males and three females, ranging in age from two years and two months to approximately six years, served as subjects in the study. In the several experiments varying numbers of these subjects were used.

4. The subjects readily learned to manipulate the tokens in obtaining food from a vender, to discriminate between tokens with and without food value, and to operate the work apparatus. That the tokens, by virtue of their use in the preliminary training, came to function as secondary or surrogate rewards was demonstrated.

5. For three out of four subjects the tokens were about as effective as was food in eliciting a work-task when measured either in terms of speed of doing a fixed task or in terms of amount of work done within a stated time interval. The fourth subject did more and faster work for food than for tokens. For three of the four subjects the variability in speed of working was slightly greater when the incentives were tokens than when they were food.

6. The tokens were effective as incentives in the delayed primary reward situations provided there was no long delay between the insertion of the tokens into a vender and the appearance of food. The condition most favorable to the elicitation of a single work act in the delayed reward situations was the one in which the subject secured a token, kept it during an interval of delay and finally exchanged it for food. Little difference was shown among the other three conditions in which the subjects either executed the work-task and waited until the end of a period for food, executed the work-task and waited with valueless tokens in their presence until the end of a delay, or worked for a token, inserted it into a vender and then waited for the food-reward.

7. Of the three situations in which the subjects could work for a period of time and at the end of that time receive from a vender food-reward in proportion to the amount of work done, the two situations most and about equally favorable to work were those in which tokens and grapes were used as incentive in the work apparatus. The third situation which offered no incentive in the work apparatus was not very conducive to work.

8. The number of tokens a subject had in its possession was one of the factors determining how many tokens would be worked for during a fixed period of time when none of the tokens could be exchanged for food until the end of the period. The more tokens possessed, the fewer additional tokens would the subjects work to secure.

9. In the discrimination situations chimpanzees (*a*) learned to select of two tokens the one which had twice the reward value of the other, (*b*) selected tokens in harmony with a hunger or a thirst drive provided the drives were fairly intense, and (*c*) associated tokens with certain activity-privileges.

10. In social situations the tokens elicited competitive behavior similar to that evoked by food. From one subject they elicited begging behavior.

11. In short, this study shows that tokens came to function as secondary or surrogate rewards for chimpanzees, that in certain situations they were about as effective as food in eliciting certain kinds of behavior, and that chimpanzees can make a variety of discriminations between tokens having different reward values and can use them in harmony with their drives or motives.

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